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THE TUBERCULARIS SPECIES GROUP OF AULACASPIS (STERNORRHYNCHA: COCCOIDEA: DIASPIDIDAE)

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Abstract

Takagi, S., 2010. The *tubercularis* species group of *Aulacaspis* (Sternorrhyncha: Coccoidea: Diaspididae). *Ins. matsum. n. s.* 66: 57–114, 29 figs.

Eight species of the scale insect genus *Aulacaspis* are recognized as belonging to the *tubercularis* species group: *A. tubercularis*, *A. alisiana*, and six new species, *A. acuta*, *A. taipingensis*, *A. alyxiae*, *A. scurrulae*, *A. scaphocalycis*, and *A. lagunae*, the first of the new species occurring in Malaysia, Singapore, and the Philippines, the last in Luzón, and the other four in Malaya. *A. tubercularis* and *A. acuta* are represented by abundant material and broadly variable in morphological characters, and the species concepts adopted in this study are tentative. *A. taipingensis* is closely related to *A. acuta*, and distinguished from the latter as another species rather tentatively. The other four of the new species appear distinct so far as represented by the available material. As a corollary of the collection data, *A. tubercularis* should originally have been a Himalayan species occurring on Lauraceae almost exclusively; it should have adapted itself to mango trees somewhere at the foot of the Himalayas, and then to mangroves in eastern Asia. *A. alisiana*, occurring in Taiwan and continental China, may be an allopatric counterpart of the Himalayan stock of *A. tubercularis*. *A. acuta* is also closely related to *A. tubercularis*, from which it should have derived somewhere in western Malesia. The new species other than *A. acuta* appear to be more or less related to the latter, from which they may have emerged directly or indirectly.

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Introduction

White Mango Scale, now treated under the name *Aulacaspis tubercularis*, is a well-known pest of mango trees. It originated somewhere in Asia and has spread to other parts of the world together with introduced mango trees. In my collection from tropical Asia I have found many forms more or less similar to it and associated mainly with wild plants. All these forms may be lumped under the *tubercularis* species group, but the boundaries of the group are not clear. The group as treated in this paper, therefore, is no more than a provisional assemblage.

It has not been easy to know how many species are represented by these forms. Eight species are recognized in this paper, but not all the species concepts thus adopted are clear and fully convincing. *A. tubercularis* itself, as understood in this paper, is not uniform. Another species is interpreted so broadly that it is impossible to prepare a simple diagnostic description applicable to all the forms referred to the species. All this, however, is not unexpected. Taxonomic studies on scale insects have been promoted, for a considerable part, with emphasis on the association of this insect group with orchards, plantations, nurseries, greenhouses, parks, gardens, and other artificial environments. Needless to say, scale insects occurring on cultivated plants are no more than fragments from the wild fauna. When abundant material is available for study from wild as well as cultivated plants, things will naturally assume much less simple aspects.

The tubercularis species group

This study is restricted to the stage of the adult female. So far as this stage is concerned, the *tubercularis* group is composed of typical *Aulacaspis* species, the full-grown adult female being of the *rosae* type, with the prosoma (the fused head, prothorax, and mesothorax) swollen and wider than the postsoma (the united metathorax and abdomen) (for the term '*rosae* type', see Takagi and Williams, 1998, and Takagi, 1999). In this group, the prosoma is a quite large mass and roughly quadrate, usually with a pair of tubercular prominences (prosomatic tubercles) on the anterolateral corners, the frontal margin being broadly rounded between them. In all the forms referred to the group, there is on the rostrum a pair of strongly sclerotized structures, which appear to hang from the 'cephalic rostral thickenings' (for this term, see Stickney, 1934) and extend caudad beyond the rostrum. In most of the species of this group, each of these 'peribuccal scleroses' ('repli péribuccal' in Balachowsky, 1954) is provided with a largely membranous appendage on the lateral side ('lateral appendage'), ending shortly (or, exceptionally, extending far) beyond the appendage. The postsoma is rather slender; usually the metathorax and the second abdominal segment are nearly the same in width and rather strongly lobed laterally, thus being a little wider than the first abdominal segment; the third abdominal segment is gently and broadly lobed laterally. Each posterior spiracle is accompanied just laterally with a few or several trilocular disc pores ('mesal group') and farther laterally with another set of disc pores ('lateral group'), which are laid on their sides and, thus, do not appear as round pores. The pygidium has an apical recess, in which the median trullae are situated except for their apices.

The prosomatic tubercles vary in shape and size during body growth, and at times not salient even in fairly grown adult females. It also occurs to mounted specimens, which are depressed dorsoventrally, that these tubercles (together with the eye spots, which primarily should be situated on the apices of the tubercles) are set back within

the general outline of the prosoma. The peribuccal scleroses are not visible in teneral specimens and represented by rudiments in growing females. Apparently, these scleroses are formed during the growth of the adult female. The derm has somewhat sclerotic patches, which are especially abundant on the prosoma. It is often not easy to determine whether they are situated on the dorsal or ventral surface; some, if not all, patches overlap between the dorsal and ventral surfaces. A short linear sclerosis appears to be associated with each anterior spiracle, located oblique anterolaterally to the spiracle; in some specimens it overlaps the cluster of disc pores associated with the spiracle, so that it should be situated on the dorsal surface (thus not particularly associated with the anterior spiracle) and may represent the boundary between the head and the prothorax. Another sclerosis, undoubtedly situated on the dorsal surface and remarkably developed, probably represents the boundary between the prothorax and the mesothorax.

Length of pygidium

As in many other Diaspididae, the adult females of *Aulacaspis* species greatly increase in body size in their long existence, and the increase takes place mainly in the prepygidial region, the pygidium remaining substantially the same in length. On the median to submarginal area, the pygidium is defined by the boundary between the fourth and fifth abdominal segments, whereas it includes the marginal area of the fourth segment; as a matter of convenience, the posterior angles of the third segment may also be included in the pygidium, each having a marginal macroduct and a pore prominence (the border of the pygidium, therefore, is not sharply definable in the submarginal area). Because the pygidium little varies in size during the growth of the adult female, its length may be adopted as a relatively stable feature. It is measured along the midline on the dorsal surface between the anterior segmental line of the fifth segment and the level of the apices of the median trullae.

Tests

In the external appearance of the test, the species of this group are generally very similar and not easily distinguishable from each other. (In one species, *A. scurrulae*, the female burrows in the leaf epidermis.) In two species, *A. tubercularis* and *A. acuta*, the female exuvial casts, especially of the second instar, are often blackish striped medially or even wholly blackish, but sometimes they are pale coloured. In some samples of these species the exuvial casts tend to be pale on tests occurring on shady parts of host plants, but in other samples this tendency is not clear. In *A. taipingensis*, too, the second-instar exuvial cast of the female is wholly darkened.

Scatter diagram and Dice-gram

Many samples are referred to *A. tubercularis* and *A. acuta*. They are variable in the numbers of wax-secreting organs, especially of the submedian and submarginal dorsal macroducts and the perivulvar disc pores. In these species, the dorsal macroducts occur on the submedian and submarginal areas of the third to fifth abdominal segments and on the submedian area of the sixth. The perivulvar disc pores are situated on the median, submedian and submarginal areas around the vulva. (In some species of *Aulacaspis* dorsal macroducts occur on more segments, and in some diaspidids there are additional groups of disc pores on the ventral surface of the abdomen.) The total numbers of these organs (rather than of the other wax-secreting organs, which occur on more restricted

parts of the body) may well characterize a specimen numerically. The combination of the sample means of these numbers may be adopted as a simple numerical index of a sample, and the relationship among samples, if any, may be visualized by plotting the sample means in a scatter diagram. (When a sample contains specimens mounted from different parts of the plant body, the sample should be divided into subsamples corresponding to the parts, and the subsample means of the numbers of the ducts and disc pores should be used as will be stated below.)

Most of the samples examined in this study were obtained from the leaves of the host plants. In some samples, specimens are also available from the branches and, except in a few cases, are more or less different from the leaf-associated specimens in the characters of the median trullae and in the numbers of wax-secreting organs. Statistical comparisons between the 'foliicolous' (leaf-inhabiting) and 'ramicolous' (branch-inhabiting) specimens (or simply 'foliicoles' and 'ramicoles'; abbreviated to 'F' and 'R' in the accompanying figures) have been made in the total numbers of the anterior spiracular disc pores, posterior spiracular disc pores, perivulvar disc pores, submedian and submarginal dorsal macrodcuts, and the macroducts and gland spines occurring on the lateral lobes of the second and third abdominal segments ('lateral macroducts' and 'lateral gland spines'). Some data are visualized by the use of Dice-gram (a population-range diagram), which shows the range, mean, and, on each side of the mean, twice the standard error and one standard deviation.

Some terms

The term 'trullae' is adopted instead of 'pygidial lobes'; the abbreviations 'abd I'–'abd VIII' stand for the first to eighth abdominal segments. In this genus, the submedian rows of dorsal macroducts are usually divided into the 'segmental series' and 'infrasegmental series'; on each segment, the segmental series is arranged along the posterior border of the segment, and the infrasegmental series is displaced anteriorly and somewhat mesally to the segmental series; on the fifth abdominal segment the division is often obscure; when some submedian macroducts are present on the sixth, they show little or no trace of the division.

The term 'sample' generally means 'specimen' or 'part of a whole'. In this paper, it is applied to all (conspecific) specimens mounted from the same lot of material. Sample means of the numbers of wax-secreting organs, however, were calculated separately for the leaf- and branch-inhabiting specimens (which form subsamples) of the same species.

Identification of host plants

The host plants except those of some samples without herbarium specimens were identified by botanists in India (Botanical Survey of India), Nepal (Department of Medicinal Plants), Malaysia (Mr K. M. Kochummen, Forest Research Institute of Malaysia; Forest Research Centre, Sabah), Singapore (Dr Hsuan Keng, University of Singapore), and the Philippines (Dr Edwino S. Fernando, University of the Philippines at Los Baños).

Type depositories

The holotypes and some other specimens of the species newly described in this paper are deposited in the following institutes. *Aulacaspis acuta*, *A. taipingensis*, *A. alyxiae*, *A. scurrulae*, and *A. scaphocalycis*: Entomology Division, Forest Research

Institute of Malaysia, Kepong, Kuala Lumpur, Malaysia. *Aulacaspis lagunae*: Museum of Natural History, University of the Philippines at Los Baños, Laguna, Philippines.

Site-Caused Variation

In not a few species of the Diaspididae, adult females occurring on the same plants but feeding on different parts of the plant body, especially on the leaves and the branches, exhibit different phenotypic characters, which are quite contrastive in some cases. In past days, variation caused by different feeding sites led to serious taxonomic confusion.

In *Aulacaspis*, a few cases of site-caused variation have been reported. In *A. ligulata*, the foliicolous and ramicolous specimens are only slightly different in the shape of the median trullae, but the ramicoles have abundant wax-secreting organs (macroducts, microducts, disc pores, and gland spines) and a strongly developed 'prosomatic outgrowth' (a feature peculiar to the species) and, thus, appear discrete from most of the foliicoles; however, intermediate individuals also occur on the leaves, connecting the other foliicoles with the ramicoles to form a broad continuous series (Takagi, 1988). In the mangrove-associated *A. australis*, the ramicolous individuals have more robust median trullae than individuals feeding on other sites, but they largely overlap the latter in the number of wax-secreting organs (Takagi and De Faveri, 2009). In a sample of *A. tubercularis* collected on the mangrove *Bruguiera sexangula*, the median trullae are broadly variable in shape and in the development of the basal zygosis through foliicolous and ramicolous individuals, one extreme of the variation being found among the foliicoles and the other among the ramicoles, whereas no obvious site-caused variation is found in the numbers of wax-secreting organs (the foliicolous specimens tend to have more dorsal macroducts, but the difference between the means is not significant statistically); in a sample from another mangrove, *Xylocarpus granatum*, the examined specimens are too few to show variation, but the median trullae seem to vary as in the sample from *Bruguiera sexangula* (Takagi and De Faveri, 2009).

The material examined in the present study was collected mainly on the leaves of the host plants. In addition to the two mangrove-associated samples of *A. tubercularis*, eight samples referable to four species have been examined for site-caused variation.

Aulacaspis taipingensis

The only sample available for the present study (with 25 foliicolous and 24 ramicolous specimens) shows no trace of site-caused variation. The median trullae are variable in shape, but the variation has no concern with the feeding sites (Fig. 22). The foliicolous and ramicolous subsamples agree exactly or nearly so in the numbers of wax-secreting organs in both the ranges and the means.

Aulacaspis tubercularis

In addition to the mangrove-associated samples studied by Takagi and De Faveri (2009), four samples collected in Nepal on the following plants have been examined for site-caused variation: an undetermined lauraceous plant ([75NPL-56], 13 foliicolous and 15 ramicolous specimens), *Lindera* sp. ([83NPL-304], 9 and 4), *Persea* sp. ([83NPL-318], 20 and 20), and *Mangifera indica* ([83NPL-375], 20 and 29).

In the first sample, the ramicolous specimens are not different from the foliicolous specimens in the state of the median trullae, which are not united basally by a distinct

zygosis in all the examined specimens. The ramicoles tend to have more wax-secreting organs than the foliicoles, and the difference between the means is statistically significant in the perivulvar disc pores and also in the anterior spiracular disc pores. In the other three samples, some specimens from the twigs have the median trullae somewhat thickened and united basally by a distinct zygosis (Fig.10 E, O), but these trullae are not so thickened as the most robust ones observed in the ramicolous forms occurring on the mangroves *Bruguiera* and *Xylocarpus* (figured in Takagi and De Faveri, 2009); other ramicolous specimens are substantially the same as the foliicolous specimens in the state of the median trullae. In each of these samples, the ramicolous and foliicolous subsamples largely overlap in the numbers of wax-secreting organs, and the ramicolous specimens tend to have more perivulvar disc pores, with the difference between the means significant (the case in the sample [83NPL-375] is shown in Fig. 1) except in the sample [83NPL-304], which is too small to test.

Another sample ([91ML-354]), collected in Malaya from *Actinodaphne sphaerocarpa*, is represented only by ramicolous specimens (over 20), which have the median trullae basally separated from each other and not united by a strong zygosis (thus agreeing with the ramicolous as well as foliicolous specimens of the sample [75NPL-56]).

Aulacaspis acuta

A sample collected in Malaya on *Cinnamomum cordatum* ([86ML-4], 50 foliicolous and 13 ramicolous specimens) is referred to this species. The ramicolous specimens differ from the foliicolous specimens in the median trullae united basally by a distinct zygosis and separated subbasally from each other by a wider space (Fig. 19). The ramicolous subsample is discrete in having more spiracular disc pores, and distinct in having much more perivulvar disc pores. In contrast, it is hardly different in the total number of the dorsal macroducts (but different in having no submedian macroduct on the sixth abdominal segment nearly always), and not distinguishable in the numbers of lateral macroducts and lateral gland spines (Fig. 2). The ramicolous specimens tend to be larger (the pygidium being about 190–250μm long) than the foliicoles (about 165–205μm).

Another sample, collected on Penang Island on *Scleropyrum wallichianum* ([91ML-495], 33 foliicolous and 2 ramicolous specimens), is referred to *A. acuta* only tentatively. In this sample, the median trullae are little different between the foliicoles and ramicoles, being not zygotic basally even in the ramicolous specimens (Fig. 18). Statistical comparisons in the numbers of wax-secreting organs are not satisfactory owing to the few ramicolous specimens, but there seem to be no such great differences as observed in the numbers of the spiracular and perivulvar disc pores in the sample [86ML-4].

Aulacaspis lagunae

In all the examined specimens (18 foliicoles and 18 ramicoles) the median trullae are zygotic basally, but in the ramicolous specimens these trullae are a little thicker and united by a stronger zygosis (Fig. 28). The foliicolous specimens have the dorsal macroducts, lateral macroducts, and lateral gland spines all tending to be more numerous, and the differences in the mean values are significant. Contrarily, they tend to have less numerous posterior spiracular and perivulvar disc pores, but the differences are not or hardly significant (the anterior spiracular disc pores are crowded so closely together that it was not always possible to count them exactly).

Summary

Seven of the eight samples mentioned above are apparently variable phenotypically in association with the different feeding sites, but not all of them vary in similar ways even in the same species. This diversity in phenotypic response, including remarkable cases, suggests the possibility that any species of the *tubercularis* group (or of the genus, in general) has potential for considerable variation in some features. When this possibility is taken into account, differences in the state of the median trullae and in the numbers of the wax-secreting organs, above all, should be evaluated very carefully in separating species.

Aulacaspis tubercularis
(Figs 1, 3, 6–10)

Aulacaspis (*Diaspis*) *tubercularis* Newstead, 1906: 73 [‘On *Cinnamomum zeylanicum*, in Java’].

Aulacaspis cinnamomi Newstead, 1908: 34 [‘On *Cinnamomum ceylanicum* (seedling plants); Molioardjo, East Java, … Also on an unknown shrub in the forest near Smeroe (Casuarinen Region); about 1,800m’].

Diaspis (*Aulacaspis*) *cinnamomi*, var. *mangiferae* Newstead, 1911: 86 [‘On small mango trees imported from Ceylon; Gizeh, Egypt’].

According to Williams (1961), Newstead described *A. tubercularis* and *A. cinnamomi* on the basis of the same material, and the name *tubercularis* is valid in spite of the meagre description. He united var. *mangiferae* or *A. mangiferae* auct. with *A. tubercularis*, because it was ‘possible to see a complete range from one extreme to another’ in Newstead’s specimens and other material from various sources.

Material examined

The samples are divided into six groups according to host plants or to plant-locality combinations. They were collected from the leaves of the host plants unless otherwise stated.

Group 1. On Lauraceae in northern India. Lachiwala, 570m, Uttar Pradesh, on *Litsea polyantha*, 8.XI.1978 [78IND-140, -143]. Grounds of the Forest Research Institute, Dehra Dun, 670m, Himachal Pradesh, on *L. polyantha* [78IND-156], *Litsea glutinosa* [78IND-158], and *Litsea lanuginosa* [78IND-160] 13.XI.1978. (These localities are situated on the outer foothills of the Himalayas.)

Group 2. On Lauraceae in Nepal. Sivapuri (or Sheopuri), 2400m, Dunche, 2000m, and Langtang Valley, 2100m, Bagmati, on *Lindera pulcherrima*, 30.VIII.1975, 17.IX.1975, and 29.IX.1975 [75NPL-111, -217, -279]. Gokarna Forest, 1350m, Kathmandu Valley, on *Lindera nacusa*, 16.X.1975 [75NPL-327]. Malepatan, 800m, Pokhara District, Gandaki, on *Lindera* sp., 7.XII.1983 [83NPL-304 (on leaves and twigs)]; Pokhara, 1300m, and Begnas Tal, 610m, Gandaki, on *Persea* sp., 9.XII.1983 [83NPL-318 (on leaves and branches), -333]. Also collected on undetermined Lauraceae at the following localities: Godavari, 1700m, Kathmandu Valley, 20.VIII.1975 [75NPL-56 (on leaves and branches)]; Dunche, 1980m, 17.IX.1975 [75NPL-218]; Sivapuri, 1830m, 19.X.1983 [83NPL-80]; Kanepokhari, 90m (in the Terai, which geographically belongs to the Gangetic Plains and extends along the outer foothills of the Himalayas), Kosi, 24.XII.1983 [83NPL-428]. (These localities except the last are situated in the Midlands of the Himalayas.)

Group 3. On montane Lauraceae in Malaysia. Gunung Jerai (altitude not recorded), Kedah,

Malaya, on *Actinodaphne sphaerocarpa*, 7.XI.1991 [91ML-354 (on branches)]. Kundasang, 1550m, Gunung Kinabalu, Sabah, on *Lindera pipericarpa*, 11.XI.1988 [88ML-326].

Group 4. On montane plants other than Lauraceae in Nepal and Malaysia. Sundarijal, 1500m, Bagmati, Nepal, on an undetermined plant of the family Celastraceae, 24.X.1983 [83NPL-107]. Cameron Highlands, 1500m, Pahang, Malaya, Malaysia, on *Ternstroemia* sp. (Theaceae), 13.X.1986 [86ML-168]. Gunung Berincang, 1900m, Cameron Highlands, on *Illicium cambodiensis* (Illiciaceae), 16.X.1986 [86ML-215]. Gunung Kinabalu, 1500m, Sabah, Malaysia, on *Polyosma* sp. (Saxifragaceae), 6.X.1988 [88ML-62].

Group 5. On mangroves. On *Rhizophora apiculata* and *Bruguiera sexangula* (both belonging to the Rhizophoraceae) and *Xylocarpus granatum* (Meliaceae) in Malaysia (Malaya; Sabah) and the Philippines (Luzón; Palawan) (for details, see Takagi and De Faveri, 2009).

Group 6. On *Mangifera indica* (Anacardiaceae). The following samples, collected on mango trees planted on the roadside, have been selected for study: Kalka, 560m, Haryana, India, 29.X.1978 [78IND-64]; Parawanipur, 90m, near Birganji, Narayani, Nepal, 18.XII.1983 [83NPL-375 (on leaves and branches)]; Kepong, Kuala Lumpur, Malaya, Malaysia, 24.XI.1985 [85ML-24]; Manila, Luzón, Philippines, 10.XII.1992 [92PL-124]; Chia-i, Taiwan, 7.IV.1965.

Sample size. The samples are represented by three to 36, mostly about 10 to over 20, mounted specimens.

Collection data

The samples of Group 1 to 4 were collected in the Himalayas and a few montane areas of Malaysia (Malaya and Sabah) on Lauraceae and a few other plants. This pattern of geographical distribution reminds me of some Himalayan taxa with their extensions into montane areas in western Malesia (which, geologically, lies on the Sunda shelf). The other samples were obtained in lowlands from mangroves (Group 5) and mango trees (Group 6). It is noteworthy that in my surveys no samples referable to *A. tubercularis* were obtained from lowland wild plants except those from the undetermined lauraceous plant in lowland Nepal ([83NPL-428], Group 2) and the mangroves in Malaysia and the Philippines. I do not think that the poor representation of samples from lowland wild plants in my collection means insufficient surveys. My surveys were carried out mainly in natural vegetation both in lowlands and on mountains and not partially to the latter, and I believe that the collection data reflect the reality to a considerable degree. (In fact, *A. acuta*, another species of the *tubercularis* group, was collected on various wild plants at many lowland localities as well as in montane forests.) In his surveys carried out in some tropical areas on Coccoidea infesting mango trees, Kondo (1996) had the impression that *A. tubercularis* was 'rather a monophagous scale on mango'. His observation is harmonious with my collection data in the lowland. In the past, *A. tubercularis* was recorded in eastern Asia not only from mango trees but also from other plants, but it should be kept in mind that there are in this region some scale insects similar to this species.

White Mango Scale (WMS), originally described as *A. cinnamomi* var. *mangiferae* and later incorporated with *A. tubercularis* (=*A. cinnamomi*), occurs on mango trees in tropical and subtropical areas of the world. It originated somewhere in Asia, and has been introduced to other parts of the world probably together with mango trees as in the case of Newstead's (1911) material. It has recently been recorded in Florida, where it occurs on a wide variety of plants (Miller and Davidson, 2005). Records of WMS on plants other than mango trees in areas where no native *Aulacaspis* species exists may be

accepted without reservation. Such records show that *A. tubercularis* is a polyphagous species (Miller and Davidson, 2005). This is contradictory to the poor representation of the species on lowland wild plants in my collection.

The collection data suggest that *A. tubercularis* occurs on mangroves broadly in eastern Asia. In general, mangrove-inhabiting scale insects should be adapted to the unique environment both ecologically and physiologically. Morphologically, the mangrove-inhabiting samples of *A. tubercularis* are somewhat peculiar in exhibiting a remarkable site-caused variation in the state of the median trullae, but otherwise they are not different from the inland samples, and there seems to be no good basis to exclude them from *A. tubercularis*. The association with mangroves, however, curiously contrasts with the poor representation of the species from inland wild plants in lowland Asia. (For further discussion, see under 'An evolutionary overview'.)

Variation: median trullae

In addition to site-caused variation, the foliicolous specimens are variable also among them. Their median trullae considerably vary in size and thickness, but they do in a virtually continuous series (Fig. 10). At one extreme of the series, these trullae are rather small and slender, being about thrice as long as wide, with the diverging mesal margins very minutely serrate or almost smooth; at the other extreme they are larger and thickened, about twice as long as wide, and finely but distinctly serrate. In foliicolous specimens, these trullae are provided at their basal extremes with a pair of small sclerites, which are set close but separated from each other by a narrow space and are connected to a pair of sclerotic dermal lines extending anteriorly for a length on the ventral surface of the pygidium (in a few samples the median trullae tend to be set so close together basally that they may appear to be yoked together, but they have no distinct zygosis). In the ramicolous specimens these sclerites are often united together to form a zygosis, which is sometimes strongly developed; in two examined samples, all the ramicolous specimens have non-zygotic median trullae, thus agreeing with the foliicolous form (see under 'Site-caused variation').

Variation: dorsal macroducts and perivulvar disc pores

The samples are variable also in the numbers of wax-secreting organs. In a diagram prepared for the correlation between the sample means (calculated separately for the foliicolous and the ramicolous subsamples) of the total numbers of the dorsal macroducts and the perivulvar disc pores (Fig. 3), the samples are scattered broadly but in a loosely bounded extent, which may be imagined to form an oblique elongate ellipse. When all the examined specimens are plotted on the diagram (this has not been done because of their very large number), they will concentrate in a large indivisible field. The samples of Group 2 (occurring on Lauraceae in Nepal) occupy the upper and lower ends as well as some intermediate areas of the imagined ellipse mostly along the supposed longitudinal axis of the ellipse. The samples of Group 1 (occurring on Lauraceae in the Indian Himalayas) and 3 (on montane Lauraceae in Malaysia) are situated about the middle of the ellipse, nearly overlapping some samples of Group 2; the samples of Group 4 (on other montane plants in Nepal and Malaysia) are scattered near the upper end of the ellipse; the samples of Group 5 (on mangroves) show some tendency to be situated on the right side, and the samples of Group 6 (on mango trees) on the left side, of the ellipse, thus being restricted to rather narrow ranges in the mean values of the numbers

of the dorsal macroducts. After all, the samples are not randomly scattered but appear to be located with some regularity on the diagram. If this apparent regularity is not false, it should imply the presence of some differentiation in association with host plants and habitats.

Variation: dorsal microducts

Dorsal microducts are usually few and restricted to the prosoma and the lateral lobes of the metathorax and the first abdominal segment, but occasionally occur also on the inner dorsal surface of the prepygidial postsoma. In one sample from Nepal ([75NPL-327]), nine out of 10 examined specimens are provided with 10 to 52 dorsal microducts on the first to third or fourth abdominal segments (Fig. 7). These microducts concentrate on the first and second segments, occurring submedially on the first segment, and submedially and often also medially on the second; a few or several microducts are often present on the third segment, occurring submedially and at times also medially; the fourth segment has no microducts except for one case, in which one microduct is present submedially on the left side of the segment. In another sample ([83NPL-428]), one out of eight examined specimens possesses a total of 53 dorsal microducts: 3 microducts occur medially on the metathorax, and 16, 20, and 14 medially to submarginally on the first to third abdominal segments, respectively. It should be emphasized that, in these samples, not all the specimens have such dorsal microducts and that there is no other character particular enough to exclude these samples from *A. tubercularis*. Furthermore, the occasional occurrence of microducts on the inner dorsal surface has also been observed in *A. acuta*.

Recognition characters

The examined samples are not uniform in host-association, habitat, and morphological variation as stated above, but no distinct morphological discontinuities have been found among them, and they are all referred to *A. tubercularis*.

The samples are commonly characterized by the pore prominences on the fourth and fifth abdominal segments represented by low, tubercular or serrate, processes and by the marginal macroducts on these segments usually less than twice as long as the longitudinal diameter of the orifice. The lateral one of the marginal macroducts occurring on the fourth segment is often shorter than the mesal one.

In the foliicolous specimens the median trullae are not zygotic, though at times they are set so close together at their bases that they may appear to be united. In the ramicolous specimens, these trullae are zygotic or not zygotic and variable in thickness: at one extreme of the variation they are robust and yoked together through a distinct basal zygosis. The second and third trullae are similar in size and shape; the mesal lobule of the second trulla is provided with a pair of long slender scleroses basally; the outer lobule of the second trulla and the lobules of the third have short obscure basal scleroses. The wax-secreting organs are variable in number. Submedian dorsal macroducts occurring on abd III–V and usually also on VI, few in each series, usually 1 (at times 0 or 2) on each side of abd VI (0 in most specimens of one sample); submarginal dorsal macroducts on abd III–V, a few to several ducts in each row; total of submedian and submarginal macroducts on both sides 19–71. Lateral lobe of abd II and also of III with macroducts rarely exceeding 10 in number; lateral gland spines nearly as numerous as lateral macroducts on each segment. Usually 2 (at times 1 or 3) marginal gland spines on

each side of abd IV (3–5 in the samples associated with *Lindera pulcherrima* in Nepal: [75NPL-111, -217, -279]). Perivulvar disc pores 61–152 in total. Anterior spiracles each with about 10–20 (rarely as many as 27) disc pores; posterior spiracles each with a few to several disc pores in each of mesal and lateral groups. Pygidium usually about 210–250µm (at times down to 200 and up to 260 or even 275µm) long.

Aulacaspis phoenicis
(Fig. 5)

Diaspis phoenicis Green, 1922: 1014 [‘On the upper surface of foliage of *Phoenix zeylanica*; Maha Illuppalama’, Sri Lanka].

Dr D. J. Williams prepared a figure of *Diaspis phoenicis* on the basis of Green’s material, and captioned it ‘*Aulacaspis tubercularis* Newstead = *A. phoenicis*. Ceylon, Maha Illuppalama on *Phoenix zeylanica*’. His figure is included in this paper with his approval (Fig. 5). So far as based on this figure, *Diaspis phoenicis* is not distinguishable from *A. tubercularis*.

Diaspis phoenicis may correctly be united with *A. tubercularis*, but it is not knowable whether, in Sri Lanka, it is an introduced scale insect or a native form representing a Himalayan element (see ‘Collection data’ under *A. tubercularis* and ‘An evolutionary overview’). Such being the case, this form is excluded from further consideration in this study.

Aulacaspis alisiana
(Figs 3, 11)

Aulacaspis alisiana Takagi, 1970: 89 [A-li Shan, Taiwan, on the leaves of *Neolitsea acuminatissima*].

Aulacaspis alisiana: Chen, 1983: 36 [Hainan Is., China, on the leaves of *Neolitsea acuminatissima*].

Aulacaspis alisiana: Tang, 1986: 206 [China: Hainan Is., on ‘*Cinnamomum assia*’ (apparently a misspelling of *C. cassia*), and E-mei Shan, Sichuan, on *Machilus bournei*].

Recognition characters (foliicolous form alone)

This species was originally described from a high altitude of Taiwan. At that time, it was compared with *A. mischocarpi* and *A. thoracica*, because it was supposed to be similar to the latter two in having robust prosomatic tubercles and a relatively slender postsoma. Chen (1983) and Tang (1986) pointed out that *A. alisiana* is close to *A. tubercularis*. I have compared the type series (15 specimens) of *A. alisiana* with a great many specimens of *A. tubercularis* now available. In *A. tubercularis* the prosomatic tubercles are usually represented by small prominences, but sometimes they are very robust (Fig. 9) as in *A. alisiana* and the two species cannot always be distinguished by the use of this feature. In other features, too, these species are very similar, and I agree with Chen and Tang in their view that *A. alisiana* is more closely related to *A. tubercularis* than to *A. mischocarpi* and *A. thoracica*. (Furthermore, *A. mischocarpi* [=*Phenacaspis mischocarpi* Cockerell and Robinson, 1914] and *A. thoracica* [=*Phenacaspis thoracica* Robinson, 1917], which were described from the same locality, probably represent one

and the same species.)

Chen and Tang state that *A. alisiana* is distinguishable from *A. tubercularis* in lacking a 'tubercular' prominence ('lateral appendage' in this paper) on each of the peribuccal scleroses. I have confirmed this character in the Taiwanese form of *A. alisiana* (Fig. 11 D), and this agreement endorses their identification of the continental form with *A. alisiana*. (In the other species of this group, the lateral appendages are usually well represented when the peribuccal scleroses are fully formed.)

A. alisiana is represented by the foliicolous form alone. It has the median trullae united basally by a small but distinct zygosis (whereas in the foliicolous specimens of *A. tubercularis* the median trullae are always separated basally from each other). *A. alisiana* is distinguishable from *A. tubercularis* also by the marginal macroducts occurring on the fourth and fifth abdominal segments: these macroducts are more than twice as long as the longitudinal diameter of the orifice, and the lateral one on the fourth segment is not shortened (whereas in *A. tubercularis* these macroducts are usually less than twice as long as the longitudinal diameter of the orifice, and the lateral one on the fourth segment is often shorter than the mesal). The dorsal macroducts are few in each of the submedian series and submarginal rows on the third to fifth abdominal segments; the sixth segment has no submedian macroduct in 19 out of 30 examined cases (that is, in 63.3%). Total of submedian and submarginal dorsal macroducts on both sides 19–32 (mean 23.9); total of perivulvar disc pores 57–106 (mean 87.1); pygidium about 225–250µm long.

In the *tubercularis* group, *A. alisiana* agrees with *A. tubercularis* and differs from the other species in having rather flat pore prominences on the fourth and fifth abdominal segments.

Aulacaspis acuta, n. sp.
(Figs 2, 4, 12–20)

Aulacaspis sp. 2, Balatibat, 1991: 51 [Mt. Makiling, Los Baños, Laguna, Luzón, Philippines, on leaves and fruits of *Litchi chinensis*].

Material examined

The samples were mounted from the leaves of the host plants, and two of them ([86ML-4] and [91ML-495]) also from the branches. They are divided into seven groups for convenience' sake.

Group 1. On Lauraceae at Bukit Nanas, Kuala Lumpur, Malaya, Malaysia. On *Beilschmiedia medang* [90ML-377, -405], *Actinodaphne sesquipedalis* [90ML-390], and *Litsea umbellata* [90ML-392], 31.VII.1990; on *A. sesquipedalis*, 3. and 23.VIII.1990 [90ML-414, -606]. Holotype: adult female, from 90ML-390.

Group 2. On Lauraceae in Malaya at localities other than Bukit Nanas and in Singapore. Tanah Rata, 1400m, Cameron Highlands, Pahang, on *Actinodaphne* sp., 13.X.1986 [86ML-171]; Gunung Berincang, 1900m, Cameron Highlands, on *Beilschmiedia* sp., 21.X.1986 [86ML-274]. Bukit Larut, 1260m, Perak, on *Phoebe grandis*, 8.X.1986 [86ML-134]. Bukit Fraser, 1300m, Pahang, on *Alseodaphne* sp., 25.X.1986 [86ML-312], and on *Actinodaphne maingayi*, 29.X.1986 [86ML-350]. Ulu Kali, 1700m, Pahang, on *Cinnamomum cordatum*, 23.IX.1986 [86ML-4 (on leaves and branches)], on *Neolitsea coccinea*, 5.X.1986 [86ML-95], and on *Actinodaphne* sp., 15.XI.1986 [86ML-484]. Grounds of the Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, on *Lindera oxyphylla*, 4.XI.1986 [86ML-395]. Pasoh Forest Reserve, Negeri Sembilan,

on *Dehaasia cuneata*, 28.IX.1986 [86ML-52]; Cape Rachado, Negeri Sembilan, on *Persea* sp., 8.XI.1986 [86ML-421, -422]. Desaru, Johor on *Litsea castanea*, 19.VIII.1990 [90ML-554]. Bukit Timah, Singapore, on *Actinodaphne malaccensis*, 5.VII.1992 [92SP-11].

Group 3. On Lauraceae in Sarawak and Sabah (Borneo Island), Malaysia. Semonggok, Kuching, Sarawak, on *Cinnanomum javanicum*, 2.X.1991 [91ML-33]. Gunung Kinabalu, 1600m, Sabah, on *Cinnamomum burmanii*, 5.X.1988 [88ML-51], and 1720m, on *Actinodaphne pruinosa*, 12.X.1988 [88ML-142].

Group 4. On Lauraceae in the Philippines. Mt. Samat, Bataan, Luzón, on *Litsea sebifera*, 29.VIII.1994 [94PL-140]. Puerto Princesa, Palawan, on *Cryptocarya ampla*, 11.VIII.1993 [93PL-53]. Maasin Forest, Brooke's Point, Palawan, on *Litsea ampla*, 23.VIII.1993 [93PL-120].

Group 5. On Dicotyledoneae other than Lauraceae. Sepilok, Sabah, Malaysia, on *Alangium ebenaceum* (Alangiaceae), 14.XI.1988 [88ML-350]. Ulu Kali, 1700m, Pahang, Malaya, Malaysia, on *Ilex* sp. (Aquifoliaceae), 5.X.1986 [86ML-100]. Grounds of the Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaya, on *Dacryodes rostrata* (Burseraceae), 4.XI.1986 [86ML-394, -399]; Kuantan, Pahang, Malaya, on *D. rostrata*, 8.VII.1990 [90ML-136]; Bukit Timah, Singapore, on *Santiria apiculata* (Burseraceae), 6.VII.1992 [92SP-28]. Bukit Tapah, 620m, Perak, Malaya, on *Sapium baccatum* (Euphorbiaceae), 19.X.1986 [86ML-249]. Gunung Jerai, 930m, Kedah, Malaya, on *Ixonanthes reticulata* (Linaceae), 5.XI.1991 [91ML-323]. Gunung Beremban, 1860m, Cameron Highlands, Pahang, Malaya, on *Helixanthera* sp. (Loranthaceae), 22.X.1986 [86ML-299]; grounds of the Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaya, on *Scurrula ferruginea* (Loranthaceae), 29.VII.1990 [90ML-346]. Cape Rachado, Negeri Sembilan, Malaya, on *Artocarpus integer* (Moraceae), 10.XI.1986 [86ML-448]. Grounds of the Forest Research Institute of Malayasia, Kepong, Kuala Lumpur, Malaya, on *Nephelium lappaceum* (Sapindaceae), 27.XI.1985 [85ML-46, among specimens of *A. scaphocalycis*]. Maasin Forest, Brooke's Point, Palawan, Philippines, on *Sterculia rubiginosa* (Sterculiaceae), 22. and 24.VIII.1993 [93PL-114, -140].

Group 6. On Monocotyledoneae. Tanjong Gelang, Kuantan, Pahang, Malaya, Malaysia, on *Pandanus* sp. (Pandanaceae), 9.VII.1990 [90ML-153]. Pagbilao, Quezon, Luzón, Philippines, on *Nypa fruticans* (Arecaceae), 3.VIII.1992 [collected by Vibien J. Calilung-Fernando]; Suqui, Calapan, Mindoro, Philippines, on *N. fruticans*, 12.VIII.1994 [94PL-19].

Group 7. Referred to *A. acuta* tentatively. Bagac, Bataan, Luzón, Philippines, on *Lepisanthes tetraphylla* (Sapindaceae), 23.VIII.1994 [94PL-102]; Mariveles, Bataan, on *L. tetraphylla*, 26.VIII.1994 [94PL-122, -132]; Mt. Samat, Bataan, on *L. tetraphylla*, 27.VIII.1994 [94PL-137]. Puerto Azul, Ternate, Cavite, Luzón, on *Lepisanthes fruticosa*, 9.XII.1992 [92PL-114, -115]. Volcano Mayon, 850m, Albay, Luzón, on *Guioa* sp. (Sapindaceae), 29.XI.1992 [92PL-51].

Group 8. Referred to *A. acuta* tentatively. Bukit Cendana, Pulau Pinang (Penang Is.), Malaya, Malaysia, on *Scleropyrum wallichianum* (Santalaceae), 21.XI.1991 [91ML-495 (on leaves and a twig)].

Sample size. Many samples contain about 10 to 30 mounted specimens; several samples are represented by a few and one sample by 63 specimens.

Collection data

The host plants recorded above belong to 11 dicotyledonous and two monocotyledonous families. This diversity of host plants may arouse doubts whether the samples mentioned above really belong to the same species. In fact, these samples as a whole are broadly variable in morphological characters. However, they are not distinguishable into distinct units, and seem to form a biologically significant group, which is treated here as a

species.

The host plants include many species of Lauraceae as in *A. tubercularis*. *A. acuta* differs from *A. tubercularis* in occurring on diverse plants in lowlands as well as on mountains. It is recorded from an undetermined species of *Pandanus* growing by the seaside and also from the back-mangrove *Nypa fruticans*, but it has not been found on mangroves. I did not collect it on mango trees, either (though in my surveys I was not particularly concerned with mango trees and other cultivated plants). I got no material referable to this species in Nepal (in my trips of a total of six months in Central and East Nepal) and India. This is especially noteworthy when compared with the common occurrence of *A. tubercularis* in the Himalayas.

Group 1: type form (Figs 4, 12, 13)

Bukit Nanas, a hill situated at the centre of the city of Kuala Lumpur, has a patch of natural forest on its northeastern side. The samples of Group 1 were collected in the forest on lauraceous plants, and probably belong to the same local population. The description given below is based on a total of 90 specimens from all these samples, and one of the specimens is designated as holotype. They are treated here in a block, representing the type form of *A. acuta*. Furthermore, no samples of *A. acuta* were obtained from other plants at this locality.

The examined adult females are fairly uniform. Marginal macroducts much elongated; those on abd IV and V twice or more as long as longitudinal diameter of orifice. On each of these segments, the mesal one of the marginal macroducts is accompanied with an acute pore prominence, which is produced in a triangle beyond the general outline of the pygidium. Median trullae longer than wide, rather robust, basally with a pair of small sclerites, which are set close together but not united and connected to a pair of sclerotic dermal lines extending anteriorly for a length on the ventral surface of the pygidium; their mesal margins nearly parallel to each other for about basal third to half, then divergent and finely serrate. Second and third trullae well developed and nearly same in size; mesal lobule of second trulla with a pair of long linear basal scleroses; outer lobule of second trulla and lobules of the third with basal scleroses obscure or not discernible. Prosomatic tubercles moderately produced. Anterior spiracles each with 3–11 trilocular disc pores; posterior spiracles each with 1–3 disc pores in mesal group and 2–4 in lateral group. Perivulvar disc pores: 4–16 in median, 9–18 in each anterolateral, and 5–17 in each posterolateral group; 48–79 in total (mean 60.5). Submedian dorsal macroducts on abd III–V and usually also on VI, 1–3 in each row on III and IV and usually 1 in each row on V and VI, sometimes lacking on VI. Submarginal dorsal macroducts on III–V, usually 1 or 2 in each row. Total of submedian and submarginal macroducts on both sides 14–28 (mean 20.6). Abd II and III each with 3–8 macroducts along margin of lateral lobe. Abd II with 2–9, and III with 5–9, small gland spines on or within margin of lateral lobe; IV with 1–3, usually 2, gland spines on margin. Pygidium about 170–215µm (usually less than 200µm) long.

Group 2–4 (Figs 2, 4, 14, 19, 20)

The samples of Group 2–4 were collected on lauraceous plants in Malaya at localities other than Bukit Nanas, and in Singapore, Sarawak, Sabah, Luzón, and Palawan. One of them ([86ML-4]) was obtained from the leaves and branches of the host plant, and the others from the leaves.

The foliicolous specimens of these groups agree well with the Bukit Nanas form in having elongated marginal macroducts and acute pore prominences on the fourth and fifth abdominal segments. In general, the median trullae are also shaped as in the type form, but in two samples ([86ML-95, -274]) these trullae are rather slender and little or only slightly serrate on their mesal margins (like those in the sample [90ML-153], Group 6, Fig. 20 B), and in one sample ([91ML-33]) they are enlarged, with their mesal margins divergent from the bases (like those in the sample [88ML-350], Group 5, Figs 15, 20 I, J). In a few samples of Group 2 and 3, the acute pore prominences are 'tuberculate-mucronate' (like those in the samples [90ML-153] and [94PL-19], Group 6, Fig. 21 K, L) rather than triangular.

The samples of Group 2–4 are not uniform in the numbers of wax-secreting organs, and are especially variable in the numbers of the dorsal macroducts and the perivulvar disc pores. In a few samples ([86ML-4], ramicolous subsample; [86ML-95, -274]) the sixth abdominal segment has no submedian macroduct frequently or nearly always. On a scatter diagram prepared for the correlation between the sample means of the numbers of the dorsal macroducts and the perivulvar disc pores (Fig. 4), the samples of Group 2 (occurring in Malaya and Singapore) tend to concentrate around the samples of Group 1. However, four samples, all from higher altitudes, are plotted distant from Group 1, having larger mean values (but not all samples from higher altitudes have such large values).

The samples of Group 3 (occurring in Borneo Island) and 4 (in the Philippines) are scattered on the diagram. One ([93PL-53]) of the two samples collected in Palawan Island on lauraceous plants is situated very close to the type form, whereas the specimens of the other sample ([93PL-120]) generally have more dorsal macroducts and perivulvar disc pores (total of the submedian and submarginal dorsal macroducts: 17–25, mean 21.7, in [93PL-53]; 24–40, mean 33.3 in [93PL-120]; total of the perivulvar disc pores: 34–68, mean 55.7 in [93PL-53]; 62–83, mean 73.7 in [93PL-120]; sample size 30 for each statistic). These samples nearly agree in the numbers of the other wax-secreting organs. They suggest that, even within this island, there occur populations which are remarkably different especially in the numbers of the dorsal macroducts and the perivulvar disc pores.

The sample [86ML-4] contains foliicolous and ramicolous specimens, and is discussed under the section 'Site-caused variation'. These specimens have the pore prominences on the fourth and fifth abdominal segments tending to be less salient and even tubercular, and the lateral one of the marginal macroducts on the fourth segment tending to be shortened, especially in the ramicolous specimens (Fig. 19 B–D). Thus they approach *A. tubercularis* (and also *A. taipingensis*: see Remarks under *A. taipingensis*). However, some specimens, especially from the leaves, possess small but acute triangular pore prominences. This sample, therefore, are referred to *A. acuta*, but what this sample means is uncertain. It does not mean the presence of a particular local form of *A. acuta*, because other samples ([86ML-95, -484]) were collected on other lauraceous plants at the same locality as the sample [86ML-4] and have the acute pore prominences well represented (Fig. 14) or extraordinarily strongly developed especially on the fourth abdominal segment (Fig. 19 A). The numbers of the submedian and submarginal macroducts and the perivulvar disc pores, too, do not support the view that all these syntopic samples are closely related to each other.

Many samples of Group 2–4 seem to agree with those of Group 1 in the length of

the pygidium, whereas some other samples have the pygidium about 220–250µm long at maximum.

Group 5 (Figs 4, 15, 20)

Samples collected on plants of nine dicotyledonous families other than the Lauraceae are lumped in Group 5. In accord with the diversity of the host plants they are variable in the size of the median trullae, forming a roughly continuous series (Fig. 20 C–J). In one sample ([88ML-350], Fig. 20 I, J) these trullae are comparatively very large, with their mesal margins divergent from the bases and rather roughly serrate; however, this sample is somewhat variable in the size of these trullae, and connected with other samples through another sample ([90ML-346], Fig. 20 G, H), in which the median trullae are also somewhat variable.

The pore prominences occurring on the fourth and fifth abdominal segments are also variable in development. In some samples these processes are acute but produced in various degrees; they are well developed in several samples including those from the Philippines ([93PL-114, -140]). In a few samples the pore prominences are 'tuberculate-mucronate' (like those in Group 6: Fig. 20 K, L) rather than triangular, and in a few other samples the pore prominence on the fourth segment tends to be tubercular, though that on the fifth remains acute (Fig. 20 M, N). In all the samples of this group the marginal macroducts are well elongated as in the type form.

This group is very variable in the numbers of wax-secreting organs. On the scatter diagram (Fig. 4), the samples are broadly scattered, but several of them (including the samples [93PL-114, –140] from Palawan Island) are situated near the type form. This group seems to be variable also in the length of the pygidium, in a few samples the pygidium being about 230–240µm long at maximum.

'*Aulacaspis* sp. 2' described by Balatibat (1991) as occurring on *Litchi chinensis* in Luzón Island is referable to *A. acuta*. So far as based on his description and illustration it is near to some samples of Group 4 and 5 in the total numbers of the dorsal macroducts and the perivulvar disc pores. It usually has no submedian macroduct on the sixth abdominal segment, but this is also the case with a few samples of Group 2.

Group 6 (Fig. 4, 20)

The three samples of this group were collected in maritime environments on the monocotyledonous plants *Pandanus* and *Nypa*. In them, the median trullae are rather slender, with the mesal margins little or slightly serrate (Fig. 20 A, B), and the pore prominences occurring on the fourth and fifth abdominal segments are tubercular with a pointed process on the lateral side ('tuberculate-mucronate') (Fig. 20 K, L). The specimens from *Nypa* are also characterized by the median trullae widely separated from each other subbasally (Fig. 20 A).

On the scatter diagram (Fig. 4), the three samples are situated very close to each other, practically agreeing in the numbers of the perivulvar disc pores and the submedian and submarginal macroducts. They nearly agree also in the numbers of the other wax-secreting organs. Their agreement in the numbers of these organs is noteworthy, because the *Pandanus*- and *Nypa*-associated forms were collected at the localities distant from each other (Malaya and Luzón). In a view, this group should represent a particular form or a species adapted to living on monocotyledons under maritime conditions. The available samples, however, are too few to support this view. In another view, it merely

represents one extreme of a continuous variation in the shape of the median trullae (Fig. 20 A–J) and, thus, is not distinguishable from the other groups of *A. acuta*. All the examined specimens possess 'tuberculate-mucronate' pore prominences on the fourth and fifth abdominal segments (Fig. 20 K, L), but such pore prominences occur also in Group 2 and 5 sporadically. They agree with the other groups of *A. acuta* in having the marginal macroducts generally well elongated. Pygidium about 180–235µm long.

Group 7 and 8 (Figs 4, 16–18)

The samples of Group 7 were collected on Luzón Island, the Philippines, whereas the only sample of Group 8 was obtained on Penang Island, Malaya, about 2500km distant from the Philippines. All these samples, however, have some characters in common, so that they are treated under the same heading. The samples associated with *Lepisanthes* were collected on the western side, and the sample associated with *Guioa* was obtained on the eastern side, of Luzón Island, but both these plant genera belong to the Sapindaceae. The sample of Group 8 differs from the Luzón forms in host association, occurring on *Scleropyrum*, Santalaceae. These samples are referred to *A. acuta*, but they differ from the other samples of *A. acuta* in having much more dorsal macroducts (Fig. 4). Furthermore, they tend to have more perivulvar disc pores, lateral macroducts, gland spines, and spiracular disc pores than many other samples. The dorsal macroducts are numerous disproportionately to the perivulvar disc pores so that on the scatter diagram (Fig. 4) these samples do not harmoniously join with Group 1–6, of which the sample means are scattered in a broad but loosely bounded extent, occupying their own field. All the samples of Group 7 and 8 have the pygidium larger than in the samples of Group 1 and many samples of Group 2–6, being about 230–250µm, sometimes up to 270µm or even 290µm, long.

One sample of Group 7 ([94PL-137], on *Lepisanthes*) and one sample of Group 4 ([94PL-140], on *Litsea*) were collected at the same spot on Mt. Samat in the Bataan Peninsula. They are discrete from each other in the total number of the submedian and submarginal macroducts (49–70, mean 60.4, sample size 14 in [94PL-137]; 30–44, mean 37.3, sample size 3 in [94PL-140]), while broadly overlapping with each other in the numbers of the perivulvar disc pores, lateral macroducts, gland spines, and the spiracular disc pores. The clear discontinuity in the number of the dorsal macroducts suggests the possibility that these syntopic (but 'allophytic') samples did not belong to the same population, and the view may be adopted that they represent different species. However, another case of remarkably different syntopic forms happens in two samples of Group 2 ([86ML-4, -484], see under Group 2–4), which are, nevertheless, referred to *A. acuta*, because they are among broadly variable samples associated with Lauraceae in Malaya.

The samples of Group 7 and 8 are not uniform in the numbers of wax-secreting organs. The samples associated with *Lepisanthes* represent two local forms separated by Manila Bay, one from the Bataan Peninsula and the other from Puerto Azul, Cavite, and these forms are fairly different in the total number of the submedian and submarginal macroducts (Fig 4). This difference is reflected in the number of the submedian macroducts occurring on the sixth abdominal segment: in the Bataan form this segment has one submedian macroduct on each side (as usual in the samples of the other groups), whereas the Puerto Azul form possesses two (or rarely one or three). The sample associated with *Guioa* is intermediate between the local forms associated with *Lepisanthes* in the total number of the submedian and submargianl macroducts, and has

one or two submedian macroducts on each side of the segment. The sample associated with *Scleropyrum*, having very numerous submedian and submarginal macroducts (total 66–104; mean 89.0 in 33 foliicolous and also in 2 ramicolous specimens), is provided with three or four (or rarely one or five) submedian macroducts on each side of the sixth segment. So far as the abundance of the macroducts is concerned, it is questionable if the sample from Penang Island has any particular relationship to the samples occurring on Luzón Island.

In the characters of the marginal features of the pygidium, the samples of Group 7 and 8 are not easily distinguishable from the other samples referred to *A. acuta*. The median trullae, above all, are shaped like in some other samples. The sample collected on *Scleropyrum* is, as stated above, especially characteristic in having abundant dorsal macroducts in both the foliicolous and the ramicolous specimens; nevertheless, in the shape of the median trullae, it well fits in the continuous series of variation formed by samples referred to the species (Figs 18, 20 E). In the sample collected on *Guioa* the median trullae appear zygotic owing to the space between their bases somewhat sclerotic, but the sclerites on their bases are clearly separated from each other, each being connected to a sclerotized dermal line extending anteriorly (Fig. 17), as in the foliicolous specimens of the other samples.

The samples of Group 7 have the pore prominences occurring on the fourth and fifth abdominal segments generally acute as usual in *A. acuta*. In the sample of Group 8, the pore prominence of the fourth segment is tubercular rather than triangular in many specimens, but that of the fifth segment remains acute (Fig. 18). Furthermore, as stated previously, tubercular pore prominences occur also in other groups sporadically. The marginal macroducts occurring on the fourth and fifth abdominal segments are generally elongated as in other samples; in the sample of Group 8 the lateral one of the marginal macroducts occurring on the fourth segment tends to be shortened, but the mesal macroduct on the segment is about twice or more as long as the orifice.

In one sample collected on *Lepisanthes* ([94PL-132]), four out of 31 examined specimens have submedian dorsal microducts on the first abdominal segment (two or three microducts) or on the first and second (five or 12 in total). The occasional occurrence of microducts on the inner dorsal surface of the prepygidial postsoma has also been observed in *A. tubercularis*. In both species, the occurrence of such microducts falls under the category of individual variation in the same samples.

The peribuccal scleroses are extraordinarily elongated in a few specimens of the sample collected on *Scleropyrum*, the longest of them being much longer than the mouth-parts (Fig. 18 E). These scleroses are formed during the growth of the adult female body. It is unknown whether in this sample the peribuccal scleroses always reach such a length ultimately.

In the samples of Group 7 and 8, the pygidium tends to be larger than in the other groups, being about 230–290μm long.

After all, the samples of Group 7 and 8 are not clearly distinguishable from the other samples referred to *A. acuta* in main features other than the number of the dorsal macroducts. In the section 'Site-caused variation', it is shown that a difference in the number of the macroducts, disc pores, or the gland spines alone affords no secure ground for separating species. Group 7 and 8 are indeed remarkably different from the other groups in having abundant dorsal macroducts, but they are isolated only in this character. In this paper I prefer to refer all the samples of Group 7 and 8 to *A. acuta*, but only

tentatively.

Recognition characters

This species as treated in this paper is so variable, including even some forms doubtfully referred to the species, that it is impossible to prepare a diagnostic description applicable to all the examined samples. It is closely related to *A. tubercularis*, and in comparison with the latter it is typically characterized by the marginal macroducts and pore prominences: on the fourth and fifth abdominal segments, the marginal macroducts are about twice or more as long as the longitudinal diameter of the orifice; on each of these segments, the pore prominence associated with the mesal one of the marginal macroducts is produced into an acute triangular process beyond the general outline of the pygidium.

These characters, however, are not always stable, and variation occurs rather sporadically. The lateral one of the marginal macroducts on the fourth segment may be shortened and the acute pore prominences may be reduced to merely angulate or rather tubercular processes. The other marginal macroducts remain stable in length and the pore prominences are reduced not uniformly in all specimens in a sample. In some specimens or in some samples, these prominences are tubercular with a pointed process on the lateral side ('tuberculate-mucronate').

The type form has the submedian and submarginal macroducts and the perivulvar disc pores less numerous than in *A. tubercularis*. The other samples referred to *A. acuta*, however, are as a whole broadly variable in the numbers of these macroducts and disc pores. The other wax-secreting organs are also variable in number, but rather sporadically.

In comparison with the other species of the *tubercularis* group, the following characters should also be mentioned: median trullae in foliicolous specimens not zygotic; submedian dorsal macroducts occurring on abd III–VI, occasionally lacking on VI.

Aulacaspis taipingensis, n. sp.
(Figs 4, 21, 22)

Material examined

Lake Garden, Taiping, Perak, Malaya, Malaysia, on leaves and twigs of *Cinnamomum iners* (Lauraceae), 10.X.1986 [86ML-146]; 25 foliicolous and 25 ramicolous specimens have been examined. Holotype: a foliicolous specimen belonging to Type P (see below).

Female test with the second exuvial cast dark brown.

Recognition characters

This form is very close to *A. acuta*, but tentatively separated from the latter (see Remarks). The median trullae are united basally through a well-developed zygosis in both the foliicolous specimens and the ramicolous specimens. They represent two types, 'Type P' and 'Type D': in Type P their mesal margins are parallel for about basal third, and then divergent to the apices (Fig. 22 A, C); in Type D the mesal margins are strongly divergent from the bases (Fig. 22 B, D); trullae intermediate between these types have also been observed (Fig. 21 G). Trullae of Type P are frequent, only five foliicolous and two ramicolous specimens belonging to Type D and several other specimens being intermediate between these types. The marginal macroducts occurring on the fourth and

fifth abdominal segments are about 1.5–2 times as long as the longitudinal diameter of the orifice. The pore prominences occurring on these segments are small and angulate rather than acutely produced (Figs 21, 22).

Submedian dorsal macroducts occurring on abd III–V, usually 1, sometimes 2, rarely 3 in each row; abd VI usually without submedian macroduct, rarely with 1. Submarginal dorsal macroducts on abd III–V, 1 or 2, rarely 3, in each row. Total of submedian and submarginal macroducts on both sides 12–23 (12–23, mean 16.9, in foliicoles; 13–23, mean 16.9, in ramicoles). Perivulvar disc pores 4–13 in median, 9–17 in each anterolateral, and 7–17 in each posterolateral group; total 51–69 (52–67, mean 60.6, in foliicoles; 51–69, mean 60.5, in ramicoles). Abd II with 2–7, and III with 3–6 macroducts on lateral lobe. Abd II with 1–5 and III with 2–9 small gland spines on lateral lobe. Abd IV with 2, rarely 1 or 3, gland spines on margin. Anterior spiracles each with 7–17 disc pores. Posterior spiracles each with 2–9 disc pores in mesal group and 1–7 in lateral group. Pygidium about 155–190µm long.

Remarks

The sample available for study shows no trace of site-caused variation, the foliicolous and ramicolous subsamples agreeing with each other exactly or nearly so in the numbers of the main wax-secreting organs and in the length of the pygidium. This species is uniquely characterized by the median trullae representing two rather remarkably different types, Type P and D as called above, which occur in both the subsamples. Although it is unknown what this dimorphism means, intermediate trullae have also been found and there is no doubt that all the examined specimens belong to the same species.

A. taipingensis may be closely related to *A. tubercularis* and *A. acuta*. It is distinguishable from the latter two in the median trullae strongly yoked together basally even in the foliicolous form, and by the pore prominences associated with the mesal ones of the marginal ducts on the fourth and fifth abdominal segments angulate rather than acutely triangular or tubercular and scarcely projecting beyond the general outline of the pgydium. It differs from most of the samples referred to *A. acuta* also in the marginal macroducts occurring on the fourth and fifth abdominal segments tending to be shorter.

A. taipingensis is not easily distinguishable from a sample referred to *A. acuta* ([86ML-4], Fig. 19 B–D). The ramicolous form of the latter has the median trullae yoked together through a well-developed basal zygosis, the acute pore prominences often reduced into angulate processes, and the lateral one of the marginal macroducts occurring on the fourth abdominal segment tending to be shortened, and thus it is very similar to *A. taipingensis* (and, in the shape of the median trullae, to Type P). I am uncertain about whether the resemblance between the two samples has any significance or it is merely incidental. *A. taipingensis* is distinguishable from *A. acuta* so far as their foliicolous forms are compared, so that it should be separated from the latter tentatively.

A. taipingensis is also similar to *A. alyxiae* (see Remarks under *A. alyxiae*).

Aulacaspis alyxiae, n. sp.
(Figs 3, 23)

Material examined

Ulu Kali, 1700m, Pahang, Malaya, Malaysia, on *Alyxia* spp. (Apocynaceae): *A. reinwardti*

var. *pumila*, 5.X.1986 [86ML-89]; *A. pilosa*, 29.VI.1990 [90ML-89]. Females and males occurring on the lower surface of the leaves; female tests small and thin. Thirty-two specimens in total (28 from the sample [86ML-89] and four from [90ML-89]) have been examined and are treated in a block in the following description. Holotype, from the sample [86ML-89].

Recognition characters (foliicolous form alone)

Median trullae yoked together basally through a well-developed zygosis, which is deeply incised medially on the posterior margin and sometimes appears divided into a pair of sclerites; mesal margins separated from each other for about basal one third, then divergent, rounded, and serrate, extending to posterolateral angles of trullae; each trulla robust, about a half as broad as long. Marginal macroducts on abd IV and V about twice or more as long as longitudinal diameter of orifice. Pore prominences associated with mesal ones of marginal macroducts on abd IV and V little produced beyond general outline of pygidium, each represented by a small pointed process or a serrate low tubercle.

Submedian dorsal macroducts occurring on abd III–V, usually none (rarely 1) on VI: 2–4 (1 or 2 in each of infrasegmental and segmental series) on III; 1 or 2, rarely 3, on IV and 1 or 2 on V. Submarginl dorsal macroducts on abd III–V, 1–5 on III, 2–4 on IV, and 1–6 on V. Total of submedian and submarginal macroducts on both sides 21–39 (mean 29.2). Perivulvar disc pores 12–22 in median, 18–30 in each anterolateral, and 14–25 in each posterolateral group; total 93–115 (mean 103.8). Anterior spiracles each with 5–14 disc pores. Posterior spiracles each with 1–6 disc pores in mesal group and 1–4 in lateral group. Abd II with 3–8 and III with 5–10 macroducts on lateral lobe. Abd II with 1–4 and III with 5–9 gland spines on lateral lobe. Abd IV with 3, at times 2 or 4, gland spines on margin. Pygidium about 225–260µm long.

Remarks

A. alyxiae is similar to *A. taipingensis* and some samples of *A. acuta* in having small and pointed pore prominences on the fourth and fifth abdominal segments in addition to the elongated marginal macroducts occurring on these segments. It has zygotic median trullae (in the foliicolous form, which alone is available), thus differing from the foliicolous specimens of *A. acuta*. The median trullae are robust, with the mesal margins curved and nearly rounded, and in this point it is more similar to *A. scurrulae* (see Remarks under *A. scurrulae*) than to *A. acuta* and *A. taipingensis*.

Aulacaspis scurrulae, n. sp.
(Figs 3, 24)

Material examined

Ulu Gombak, 600m, Selangor, Malaya, Malaysia, on leaves of *Scurrula ferruginea* (Loranthaceae), 1.X.1986 [86ML-75]. Females and males occur on the scurfy-tomentose lower surface of the leaves. Females burrow in the leaf-epidermis, each forming a blister-like swelling on the leaf surface. The present study is based on 17 mounted specimens of the adult female.

Recognition characters (foliicolous form alone)

Median trullae robust, yoked together through a distinct basal zygosis, which is deeply incised medially on the posterior margin; mesal margins separated from each

other for about basal third, then divergent, rounded, and serrate, extending to apices near posterolateral angles of trullae. Mesal lobules of second and third trullae each with a pair of distinct linear scleroses basally. Marginal macroducts shortened; those on abd IV and V about 1–1.5 times as long as longitudinal diameter of orifice. Pore prominence associated with mesal one of marginal macroducts on each of abd IV and V low and broad, with a small pointed process medially, that on IV broader. Prosomatic tubercles prominent, deltoid in shape. Peribuccal scleroses slender even on full-grown adult females.

Submedian dorsal macroducts occurring on abd III–V, lacking on VI, 1 in each of infrasegmental and segmenal series on III, 1 or 2 on IV, usually 1, rarely 0 or 2, on V. Submarginal dorsal macroducts on abd III–V, 1 or 2 on III, 1 or 2, rarely 3, on IV, 1–3 on V. Total of submedian and submarginal macroducts 12–24 (mean 18.2). Perivulvar disc pores 8–14 in median, 16–28 in each anterolateral, and 14–29 in each posterolateral group; total 78–116 (mean 101.1). Anterior spiracles each with 4–12 disc pores; posterior spiracles each with 1 or 2 disc pores in mesal and 1–3 in lateral group. Abd II with 6–13 and III with 5–11 macroducts along margin of lateral lobe. Abd II with 4–8 and III with 5–10 small gland spines within margin of lateral lobe; abd IV with 1 or 2 gland spines on margin. Pygidium about 230–260µm long.

Remarks

A. scurrulae has the median trullae rounded and serrate on their mesal margins probably in association with its habit to burrow in the leaf epidermis. It is characteristic also in having short marginal macroducts, and this character may also be adaptive to the habit. It is somewhat similar to *A. alyxiae* in the shape of the median trullae, but the latter does not burrow and has longer marginal macroducts. The significance of the robust median trullae in *A. alyxiae* is, therefore, unknown.

Two other species of *Aulacaspis* occur on *Scurrula ferruginea* in Malaya. In one of them, the females burrow under the epidermis on the twigs and the lower surface of the leaves, but have the median trullae not so robust and rounded as in *A. scurrulae*. The other species is *A. acuta*: one sample was collected on S. *ferruginea* ([90ML-346]), the females and males occurring on the glabrous upper surface of the leaves.

Aulacaspis scaphocalycis, n. sp.
(Figs 25–27)

Material examined

The samples were collected from the leaves of the host plants. They are divided according to the localities and host plants as follows.

Group 1. Grounds of the Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, on *Scaphocalyx spathacea* (Flacourtiaceae), 22.XI.1985 [85ML-10], 30.X.1991 [91ML-300]. Holotype, from 91ML-300.

Group 2. Bukit Nanas, Kuala Lumpur, Malaya, Malaysia, on *Scaphocalyx spathacea*, 3, 5, 23.VIII.1990 [90ML-403, -434, -594]; on *Ryparosa fasciculata* (Flacourtiaceae), 23.VIII.1990 [90ML-583].

Group 3. Grounds of the Forest Research Institute of Malaysia, on *Nephelium lappaceum* (Sapindaceae), 27.XI.1985 [85ML-46, together with *A. acuta*].

Group 4. Bukit Fraser, Pahang: 1300m, on *Sandoricum koetjape* (Meliaceae), 26.X.1986

[86ML-329]; 1000m, on *Xanthophyllum* sp. (Polygalaceae), 28.X.1986 [86ML-345].

Sample size. Group 1 is represented by a total of 21 mounted specimens, and Group 2 by 32. The samples of Group 3 and 4 are small, each having three to five specimens, and not all of the specimens are in good condition.

Group 1 (Fig. 25)

The two samples, collected on the leaves of the same plant species and at the same locality in 1985 and 1991, show no substantial difference, so that they are treated in a block. Full-grown adult female sclerotic throughout; prosomatic tubercles roundish or nearly deltoid; postsoma tending to be narrower posteriorly. Median trullae not zygotic, mesal margins separated from each other by a slender space for about basal third to half, then divergent to blunt or round apices and serrate; basal extremities connected to a pair of short sclerotic dermal lines extending anteriorly on ventral surface. Second and third trullae similar in size and shape; inner lobule of second trulla with a pair of long slender basal scleroses. Marginal macroducts occurring on abd IV and V about twice or less as long as longitudinal diameter of orifice. Pore prominences associated with mesal ones of marginal macroducts on abd IV and V small and pointed. Submedian dorsal macroducts occurring on abd II–VI, distinctly separated into segmental and infrasegmental series on II–IV; 2–6 in segmental and 1–5 in infrasegmental series on II, 2–5 and 1–5 on III, 1–4 in each series on IV, 2–5 on V, and 1 or 2 on VI. Submarginal dorsal macroducts on abd III–V, 3–8 on III, 2–6 on IV, and 3–6 on V. Total of submedian and submarginal macroducts on both sides 48–99 (mean 76.6). Perivulvar disc pores 8–18 in median, 22–34 in each anterolateral, and 11–21 in each posterolateral group; total 80–119 (mean 103.9). Anterior spiracles each with 11–21 disc pores; posterior spiracles each with 2–6 disc pores in mesal group and also in lateral group. Abd II with 7–19 and III with 7–14 macroducts on margin of lateral lobe. Abd II with 6–15 and III with 7–18 small gland spines along margin of lateral lobe. Abd IV with 3, at times 2 or 4, gland spines on margin. Pygidium about 250–295µm long.

Group 2 and 3 (Figs 26, 27)

The samples of these groups tend to have less numerous submedian and submarginal macroducts (mean of total numbers 61.0–74.0) and perivulvar disc pores (mean of total numbers 84.0–88.4) than those of Group 1. However, the samples of Group 1–3 broadly overlap in the ranges of the numbers of these wax-secreting organs. The samples collected on *Ryparosa fasciculata* and *Nephelium lappaceum* have the median trullae separated from each other by a space often wider than in Group 1. Pygidium about 230–280µm long.

Group 4 (Fig. 27)

The two samples collected on Bukit Fraser, about 40km distant from Kuala Lumpur, are represented by three ([86ML-329], occurring on *Sandoricum*) and four adult females ([86ML-345], on *Xanthophyllum*). The specimens collected on *Xanthophyllum* differ from those collected in the two localities of Kuala Lumpur (Group 1–3) in having much more perivulvar disc pores (mean of total numbers 137.0) and more submedian and submarginal macroducts (mean of total numbers 97.3) and also in the pygidium larger (being about 300–330µm long). The specimens collected on *Sandoricum* are intermediate between those from *Xanthophyllum* and the samples from Kuala Lumpur in the total

number of the perivulvar disc pores (mean 126.7), but they are not substantially different from Group 1–3 in the total number of the submedian and submarginal macroducts (mean 76.7). Pygidium about 280–290µm long.

The median trullae are variable in size apparently in correlation with the size of the pygidium, but in most specimens they are similar in shape. Exceptionally, these trullae are a little broadened posteriorly in two of the four specimens collected on *Xanthophyllum* (Fig. 27 D). A similar variation in the shape of the median trullae is known in *Aulacaspis calophylli* (Takagi, 1999).

After all, the samples referred to *A. scaphocalycis* are fairly variable in several features in spite of their limited numbers, and it seems that they represent fragments from a broad variation in this species.

Recognition characters (foliicolous form alone)

Among the species referred to the *tubercularis* group, *A. scaphocalycis* is easily recognizable in having submedian dorsal macroducts on the second to sixth abdominal segments. This species (as represented by the foliicolous form alone) is characterized in common with the foliicolous forms of *Aulacaspis tubercularis* and *A. acuta* in having non-zygotic median trullae, and it is similar to some samples of *A. acuta* in having small pointed pore prominences on the fourth and fifth abdominal segments.

Aulacaspis lagunae, n. sp.
(Figs 28, 29)

Material examined

Mud Spring, Mt. Makiling, Los Baños, Laguna, Luzón, Philippines, on *Cinnamomum* sp. (Lauraceae), 6.VIII.1994 [94PL-4]. Eighteen specimens mounted from the leaves and another 18 from the branches have been examined. Holotype: foliicolous specimen.

Recognition characters

The foliicolous and ramicolous specimens are compared in the section 'Site-caused variation'. Median trullae yoked together by a distinct basal zygosis, separated from each other basally, then divergent and serrate; a little thicker with a stronger basal zygosis in ramicolous specimens. Mesal lobule of second trulla with a pair of short linear scleroses basally. Marginal macroducts occurring on Abd IV and V about twice or less as long as longitudinal diameter of orifice; mesal one of marginal macroducts on each of these segments accompanied with a small pointed pore prominence. Submedian dorsal macroducts on abd I–V, always lacking on VI, few in each series and often lacking on I especially in ramicolous specimens.

Foliicolous specimens. Submedian macroducts 1–3, at times 0, in each series on abd I; 1–5 in segmental and 1–4, at times 0, in infrasegmental series on II; 1–4 in each series on III; 1–3 in segmental and 1 or 2 in infrasegmental series on IV; 1–4 on V. Submarginal macroducts 1–4 on abd III, 2–4 on each of IV and V, rarely 1 or 2 on II. Total of submedian and submarginal macroducts on both sides 22–83 (mean 66.4). Perivulvar disc pores 13–20 in median, 20–30 in each anterolateral, and 14–29 in each posterolateral group; total 81–144 (mean 117.1). Anterior spiracles each with about 18–35 disc pores; posterior spiracles each with 4–11 in mesal and 1–4 in lateral group. Abd II with 1–7 and III with 5–8 macroducts on margin of lateral lobe. Abd II with 0–3 and

III with 6–13 gland spines along margin of lateral lobe. Abd IV with 3–7 gland spines on margin. Pygidium about 230–275µm long.

Ramicolous specimens. Submedian macroducts usually absent on abd I, at times 1 or 2 occurring in segmental and 1 in infrasegmental series; 1 or 2, at times 0, in each series on II; 1–3, at times 0, in each series on III, 1 or 2, at times 0, in each series on IV, and 1–3, rarely 0, on V. Submarginal macroducts 1–3 on III, 1–4 on IV, and 2–4 on V. Total of submedian and submarginal macroducts on both sides broadly variable owing to frequent absence of submedian macroducts, 9–52 (mean 33.8). Perivulvar disc pores 11–22 in median, 22–45 in each anterolateral, and 11–28 in each posterolateral group; total 87–161 (mean 126.6). Anterior spiracles each with about 24–50 disc pores; posterior spiracles each with 4–13 in mesal and 2–5 in lateral group. Abd II with 1, at times 0 or 2, macroducts and III with 2–7 on margin of lateral lobe. Abd II at times with 1 gland spine and III with 3–7 gland spines along margin of lateral lobe. Abd IV with 3–6 gland spines on margin. Pygidium about 215–270µm long.

Remarks

The examined sample is not stable in the occurrence of submedian dorsal macroducts especially in the ramicolous specimens, which usually have no submedian macroducts on the first abdominal segment and at times also on other segments. Owing to this frequent absence of submedian macroducts on one or more segments in the ramicolous form, the site-caused effect in this sample appears to be remarkable in the total number of dorsal macroducts. The foliicolous form is usually provided with submedian macroducts on the first to fifth abdominal segments, and on this account *A. lagunae* is recognizable as a good species among the forms of the *tubercularis* group.

An Evolutionary Overview

Eight species including six new species are recognized in the *tubercularis* group, but not all of them are clearly distinguishable owing to their variable characters. Especially, the boundaries between *A. tubercularis* and *A. acuta* and also between *A. acuta* and *A. taipingensis* are obscured by local, 'allophytic', or site-caused variation. *A. acuta* as represented by the typical form is characteristic in having acute triangular pore prominences, which are remarkably developed in some samples. In some other samples, however, they are reduced to angular or pointed processes, and similar prominences occur in the other new species.

If the species concepts adopted in this study are correct, if the *tubercularis* group as composed in the present paper is really a natural group, and if the available collection data reflect the reality to a considerable degree, some interpretations are possible on evolutionary relationships among the forms of the group.

First, the notorious White Mango Scale (WMS) or *A. tubercularis* should originally have been a Himalayan species associated with Lauraceae almost exclusively. It follows that *A. tubercularis* expanded onto *Mangifera indica* at the foot of the Himalayas, where it adapted itself to living on this plant and established its stabilized population on the plant. It has broadened its range of distribution in lowlands, especially together with mango cultivation in recent times. Raman et al. (2009), in their review of literature on certain gall-inducing insects and the origin of *Mangifera indica*, state that the land bordered by Assam, Myanmar, and Bangladesh is considered to be the epicentre of *M.*

indica. The expansion of *A. tubercularis* onto *M. indica*, accordingly, may have been possible from the time of the emergence of this plant. Of course, it is not necessary to think that the establishment of the mango-inhabiting form took place only in one area and only once. Tropical Asia abounds in native *Aulacaspis* species, and WMS there should be in a stabilized state after a long history of competition and selection. (A well-documented example of competitive displacement in diaspidids is presented by DeBach et al., 1978.)

In the Himalayas, *A. tubercularis* was collected not only on Lauraceae but also on a celastraceous plant; at high altitudes in Malaysia (and also in Java, according to Newstead, 1908), it was found on Lauraceae and a few other plants, which are not particularly closely related to the Lauraceae and to each other. These records suggest that this species potentially has ability to live on a broad range of plants. The introduction of WMS outside tropical Asia should be an unintended experiment to see if and how the expansion of WMS on other plants takes place under new ecological conditions. In Florida, WMS has realized its broad host range, and this is probably a result of its increasing populations in the environments without native *Aulacaspis* species. If this supposition is correct, WMS should be broadening its host range also in other regions of America (especially Caribbean islands, Central America, and tropical South America, where WMS has broadly been established), tropical Africa, Madagascar, and other areas where no native *Aulacaspis* species exists.

The occurrence of *A. tubercularis* on mangroves in eastern Asia is mysterious, because the species was not collected from other lowland wild plants in this region. Secondly, therefore, the only possibility adoptable on the basis of the collection data is that the mangrove-inhabiting form originated from a population or populations occurring on mango trees cultivated by the seaside (or not very far from the seaside). *Aulacaspis pallida* (=*Phenacaspis pallida* Robinson) was recorded from a mangrove at Pagbilao, Luzón. This record was attributed to an occasional dispersal of crawlers onto the mangrove from a tree of the usual host plant, *Litsea sebifera*, standing near the mangrove swamp (Takagi and De Faveri, 2009).

Thirdly, *A. alisiana* may be an allopatric counterpart of the Himalayan stock of *A. tubercularis*, occurring in Taiwan and continental China. Its range of distribution, however, is not yet well known.

A. acuta is another species that is very closely related to *A. tubercularis*. As treated in the present study, it is a variable species, some samples connecting the typical form to other species of the group. It occurs in lowlands and at higher altitudes, feeding on diverse plants including many lauraceous species, and is probably broadly distributed in western Malesia. *A. tubercularis* occurs also in this region but, except for the mango- and mangrove-inhabiting forms, it is restricted to montane areas, where it occurs on Lauraceae and other plants.

A. acuta is derivative as compared with *A. tubercularis* in the acute triangular pore prominences, because such pore prominences are not usual in the genus. Fourthly, therefore, if they have an immediate ancestor-descendant relationship, *A. acuta* should have derived from *A. tubercularis*, not vice versa, somewhere in eastern Asia. It is unknown what factor or factors contributed to the emergence of *A. acuta*, but this species has been successful and has increased its variation in western Malesia. Fifthly, therefore, *A. acuta* has probably been the stem species from which some other species of the group emerged directly or indirectly. Among the latter, *A. scurrulae* emerged apparently

as a result of adaptation to burrowing into the leaf epidermis. *A. scaphocalycis* and *A. lagunae* as compared with the other species of the group have additional submedian dorsal macroducts anteriorly to the third abdominal segment, though the ramicolous form of *A. lagunae* is not stable in the occurrence of these macroducts. These two species must have evolved under some environmental conditions that promoted the appearance of the additional submedian dorsal macroducts (which extends forward the area on the dorsal surface that produces wax filaments for test construction). *A. lagunae* was collected only at Mud Spring, a spot emitting a volcanic vapour. If this record is not meaningless, this peculiar environment possibly has a concern with the emergence and survival of this species.

The evolutionary interpretations given above are highly speculative with too many ifs. Moreover, in Indochina, the region between the Indian subcontinent and western Malesia, nothing is known about the *tubercularis* group except for a few records of the White Mango Scale on mango trees, and in eastern Malesia (east of the Macassar Strait), especially in Indonesian islands, the diaspidid fauna is desperately poorly known. In consideration of our ignorance about the faunae of these regions, which adjoin the regions surveyed in the present study, the above interpretations may not easily be accepted.

However, the present study of the *tubercularis* group is based not on occasionally obtained material but on a large number of samples collected in repeated trips. The evolutionary scenario this set of samples has brought forth — the Himalayan origin of *A. tubercularis* followed by the emergence of the other forms of the *tubercularis* group in eastern Asia — may be worthy to serve as a starting point for further investigations in this group, whether it will eventually be accepted or rejected.

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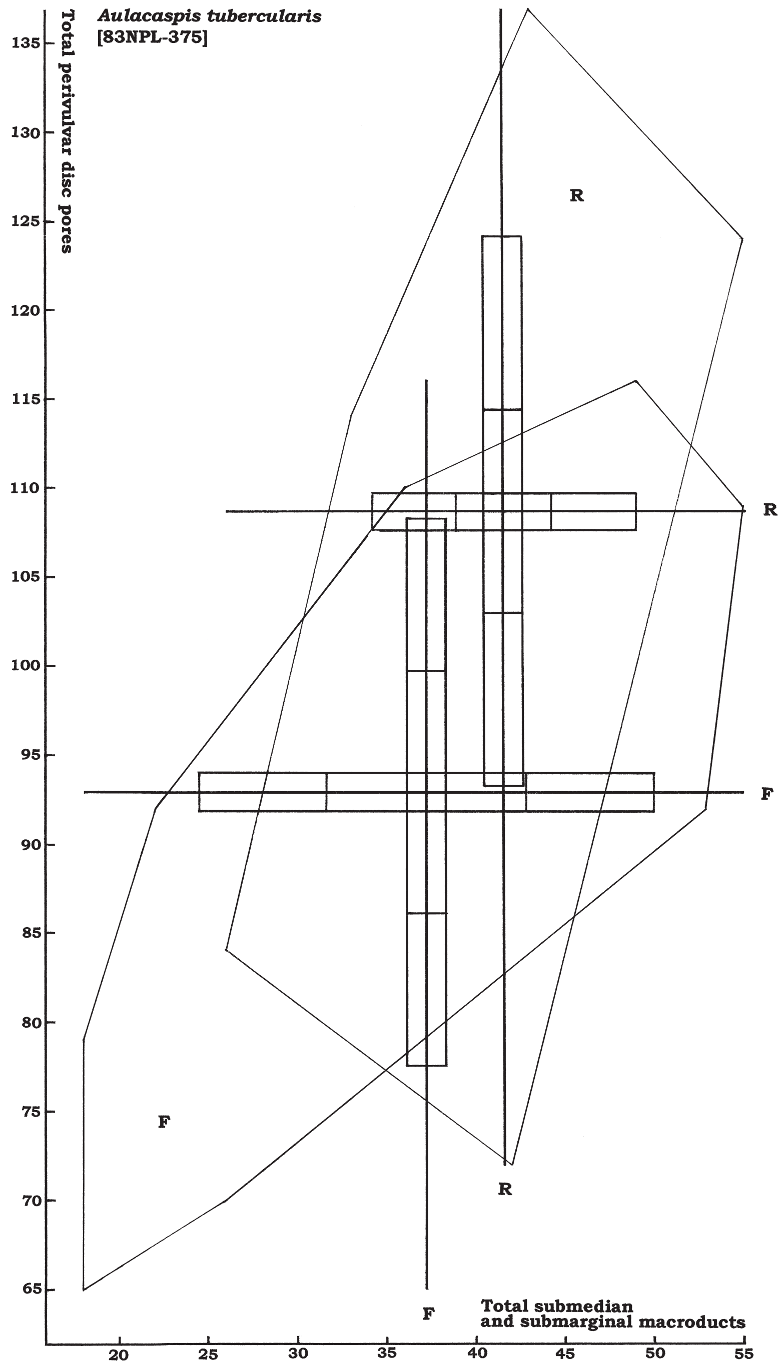

Fig. 1. *Aulacaspis tubercularis*, Parawanipur, Nepal, on *Mangifera indica* [83NPL-375], foliicolous (F) and ramicolous (R) subsamples. Dice-grams showing variation in the total numbers of the perivulvar disc pores and the submedian and submarginal macroducts. (For an explanation of the Dice-grams, see Fig. 2, Total anterior spiracular disc pores.)

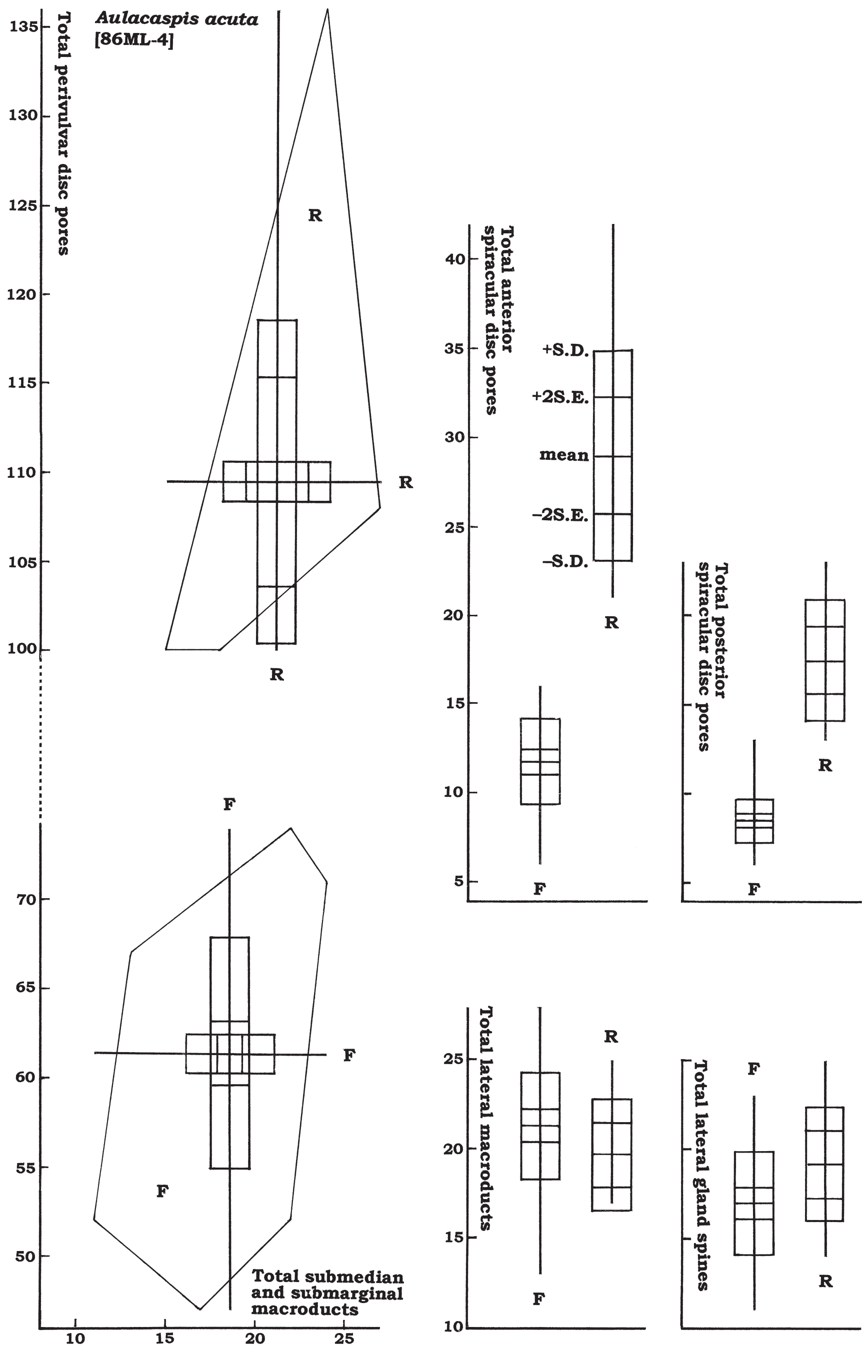

Fig. 2. *Aulacaspis acuta*, Ulu Kali, Malaya, on *Cinnamomum cordatum* [86ML-4], foliicolous (F) and ramicolous (R) subsamples. Dice-grams showing variation in the total numbers of the perivulvar disc pores, the submedian and submarginal macroducts, the anterior spiracular disc pores, the posterior spiracular disc pores, the lateral macroducts, and the lateral gland spines.

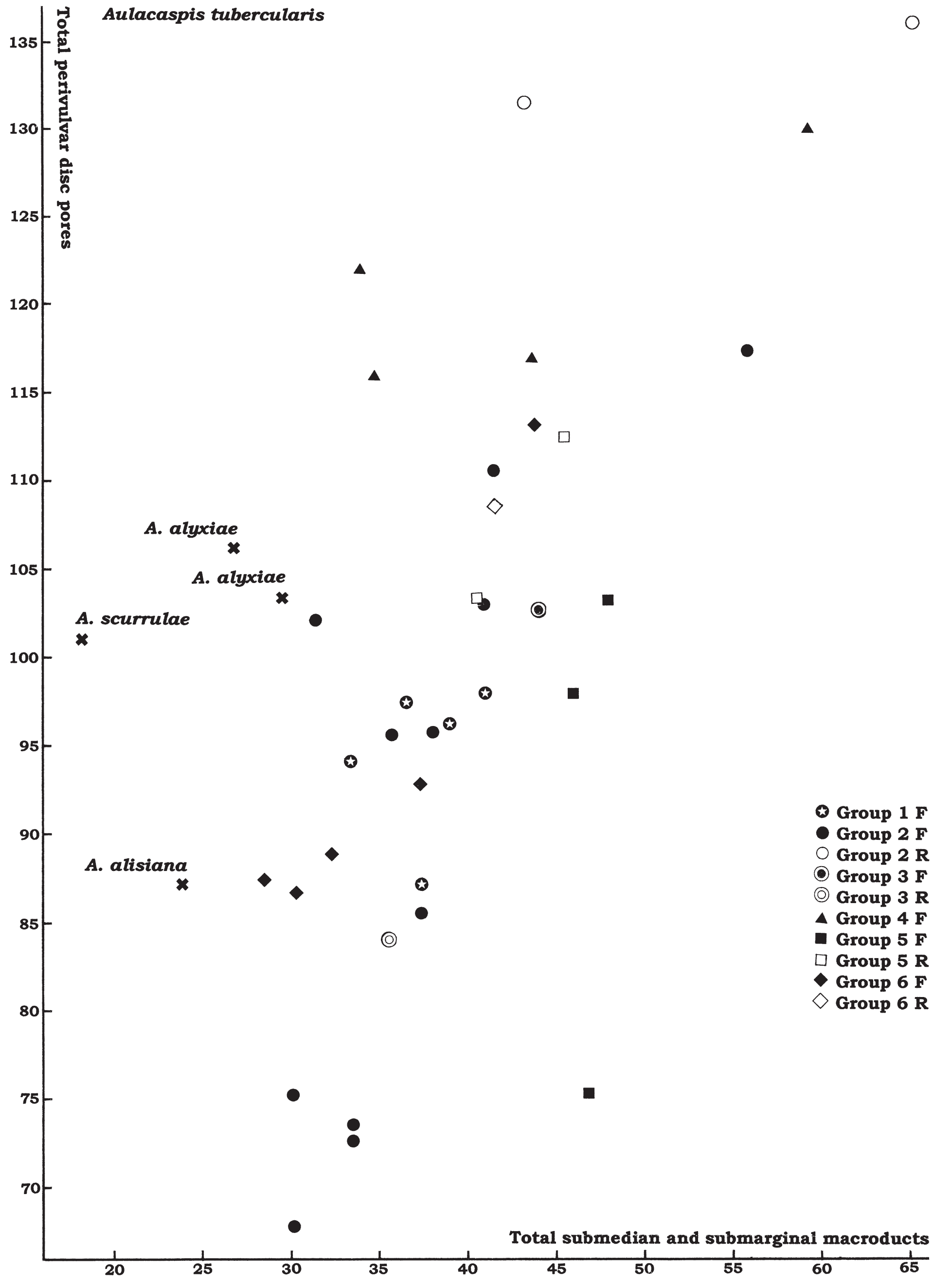

Fig. 3. *Aulacaspis tubercularis*. Scatter diagram dotted with sample or subsample means of the total numbers of the perivulvar disc pores against those of the total numbers of the submedian and submarginal macroducts. Many samples are represented only by foliicolous specimens (F); five samples are divided into foliicolous (F) and ramicolous (R) subsamples; one sample contains only ramicolous specimens (R). The samples of *Aulacaspis alisiana*, *A. alyxiae*, and *A. scurrulae* are also dotted for comparison.

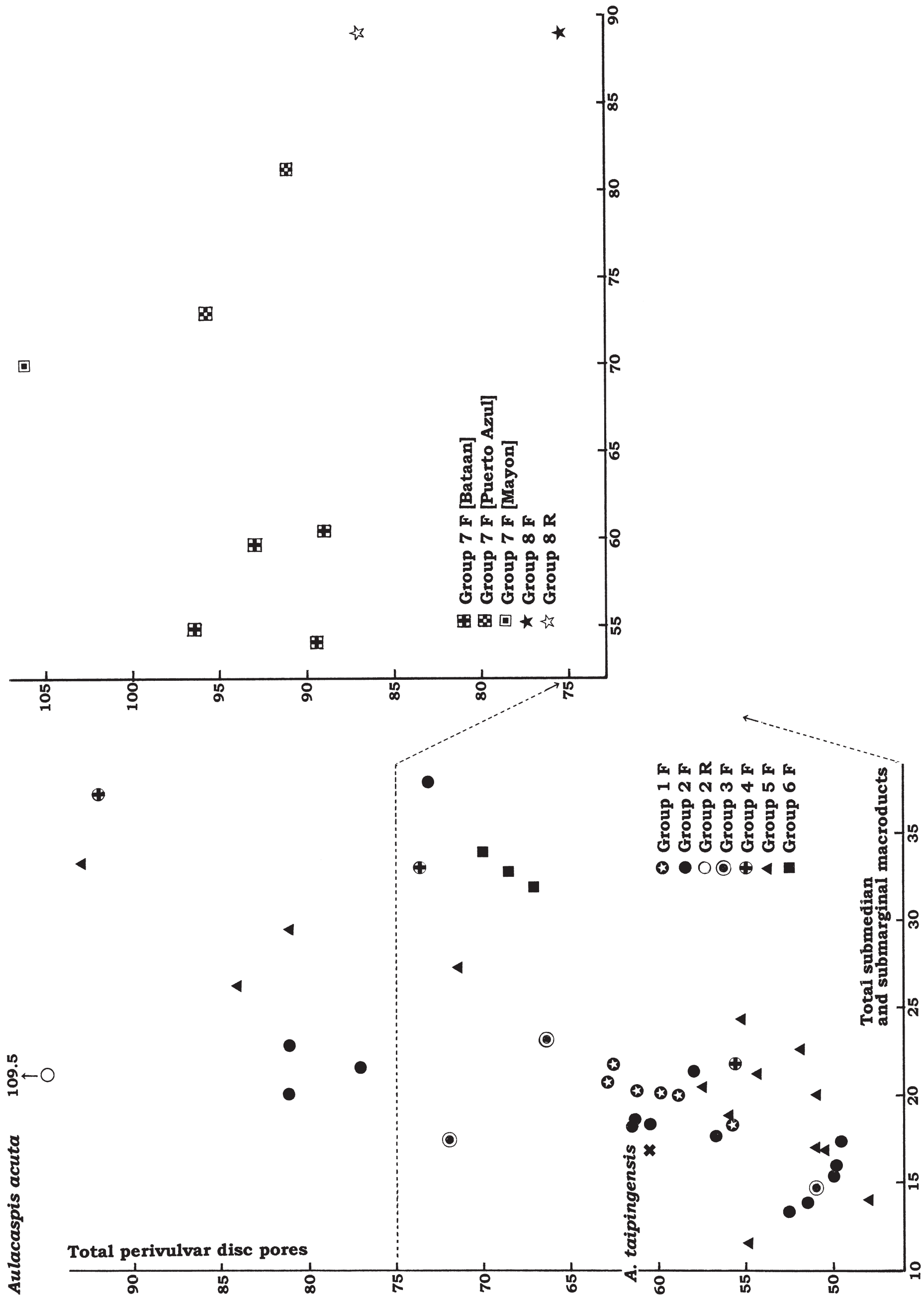

Fig. 4. *Aulacaspis acuta*. Scatter diagram dotted with sample or subsample means of the total numbers of the perivulvar disc pores against those of the total numbers of the submedian and submarginal macroducts. The samples are represented by foliicolous specimens (F) except two, which contain foliicolous (F) and ramicolous (R) subsamples. (The diagram is divided into two parts owing to the limited space.) *Aulacaspis taipingensis* is included for comparison.

Fig. 5. '*Aulacaspis tubercularis* Newstead = *A. phoenicis*. Ceylon, Maha Illuppalama on *Phoenix zeylanica*.' (Depicted and captioned by Dr D. J. Williams.)

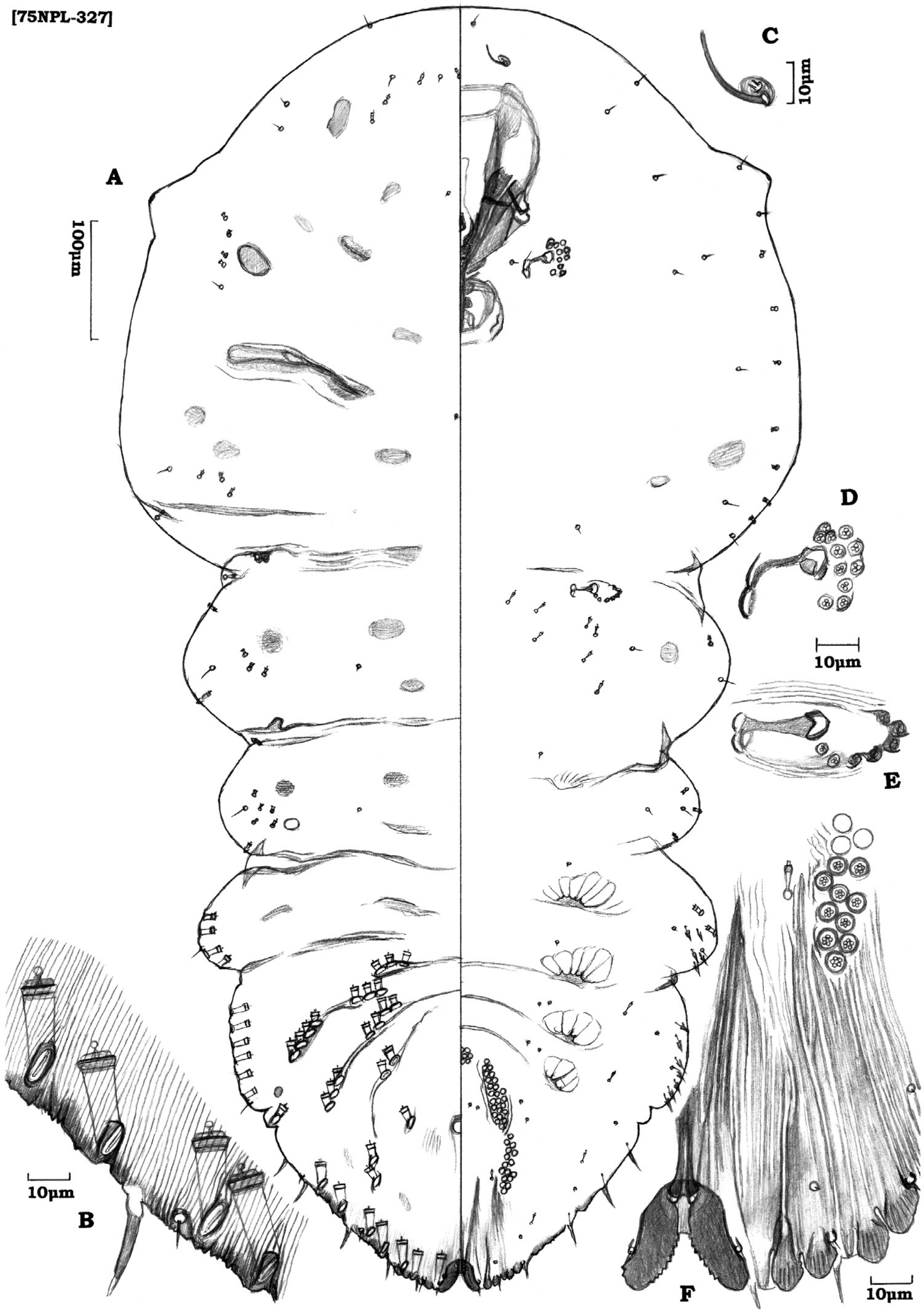

Fig. 6. *Aulacaspis tubercularis*, foliicolous specimen, nearly full-grown, but still with the derm membranous and the peribuccal scleroses rudimentary. Kathmandu Valley, Nepal, on *Lindera* [75NPL-327], Group 2. B, margin of abd IV and V, dorsal surface; C, antenna; D, anterior spiracle; E, posterior spiracle; F, trullae.

Fig. 7. *Aulacaspis tubercularis*, foliicolous specimen, with dorsal microducts on the prepygidial abdomen. Kathmandu Valley, Nepal, on *Lindera* [75NPL-327], Group 2. B, dorsal microducts; C, submarginal boss on abd I; D, margin of abd IV and V, dorsal surface; E, antenna; F, anterior spiracle; G, posterior spiracle; H, trullae.

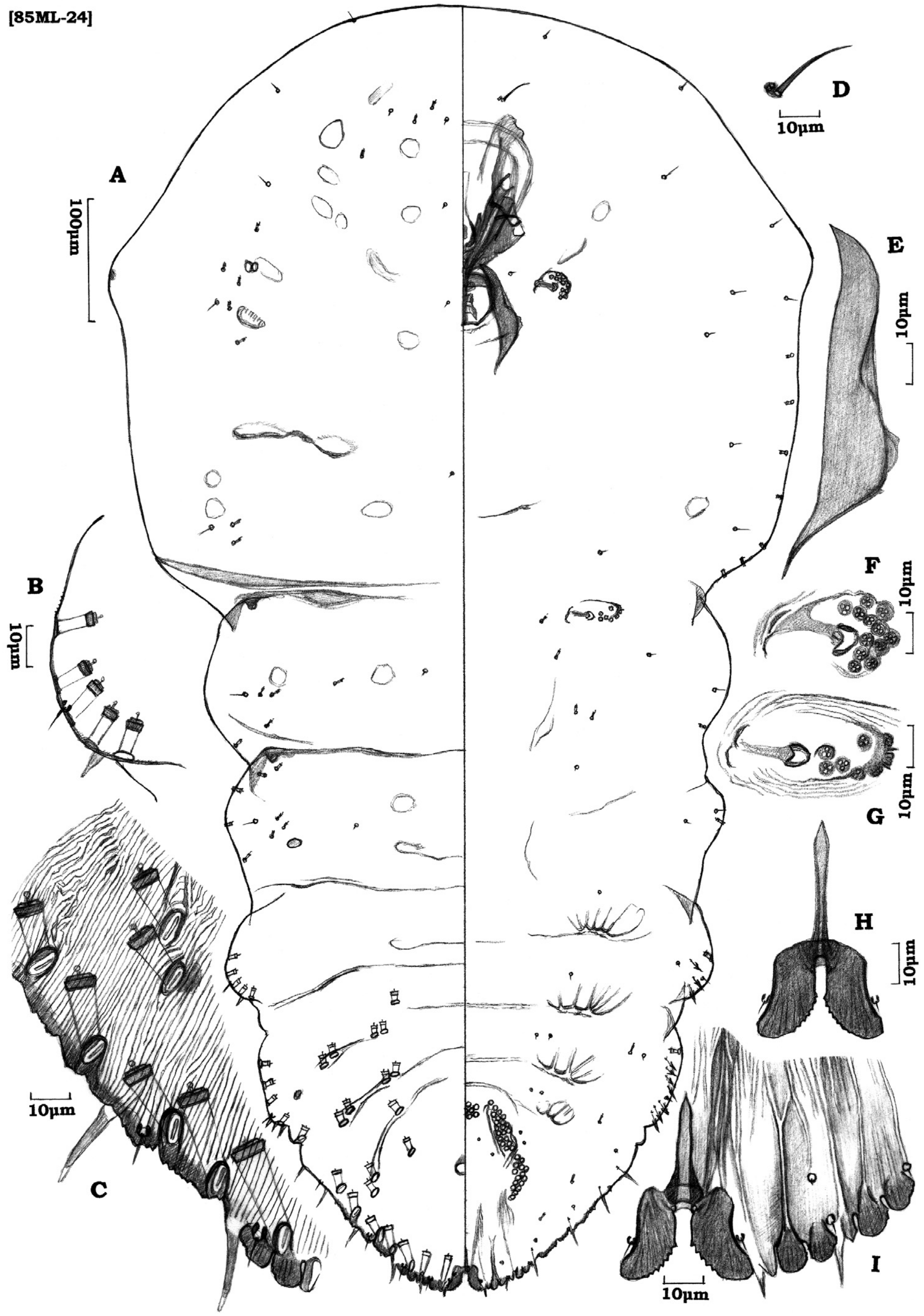

Fig. 8. *Aulacaspis tubercularis*, foliicolous specimen. Kuala Lumpur, Malaya, on *Mangifera* [85ML-24], Group 6. B, lateral macroducts on abd II; C, margin of abd IV–VI, dorsal surface; D, antenna; E, peribuccal sclerosis; F, anterior spiracle; G, posterior spiracle; H, median trullae; I, trullae.

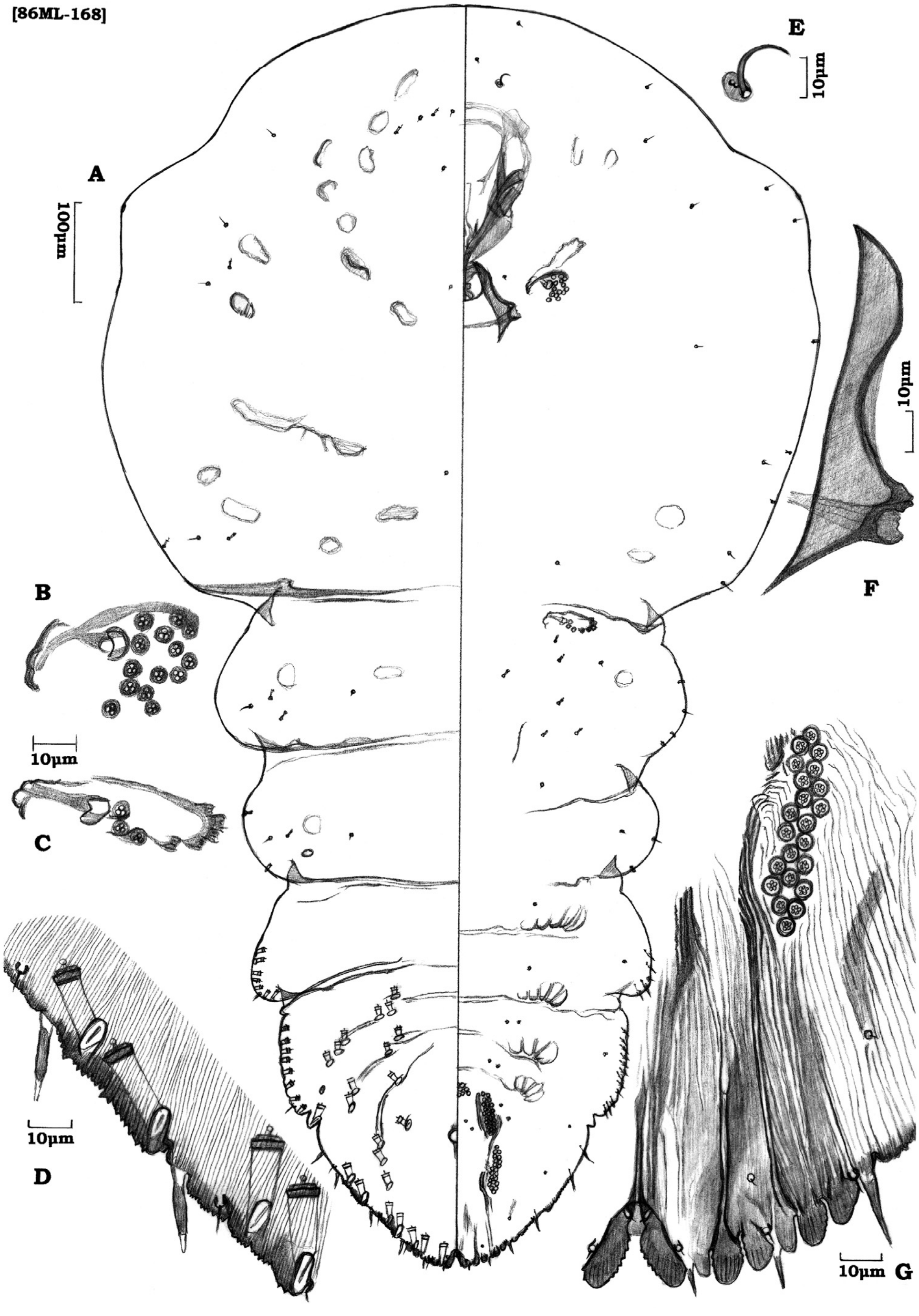

Fig. 9. *Aulacaspis tubercularis*, foliicolous specimen, with prosoma and prosomatic tubercles eminently developed. Cameron Highlands, Malaya, on *Ternstroemia* [86ML-168], Group 4. B, anterior spiracle; C, posterior spiracle; D, margin of abd IV and V; E, antenna, F, peribuccal sclerosis; G, trullae.

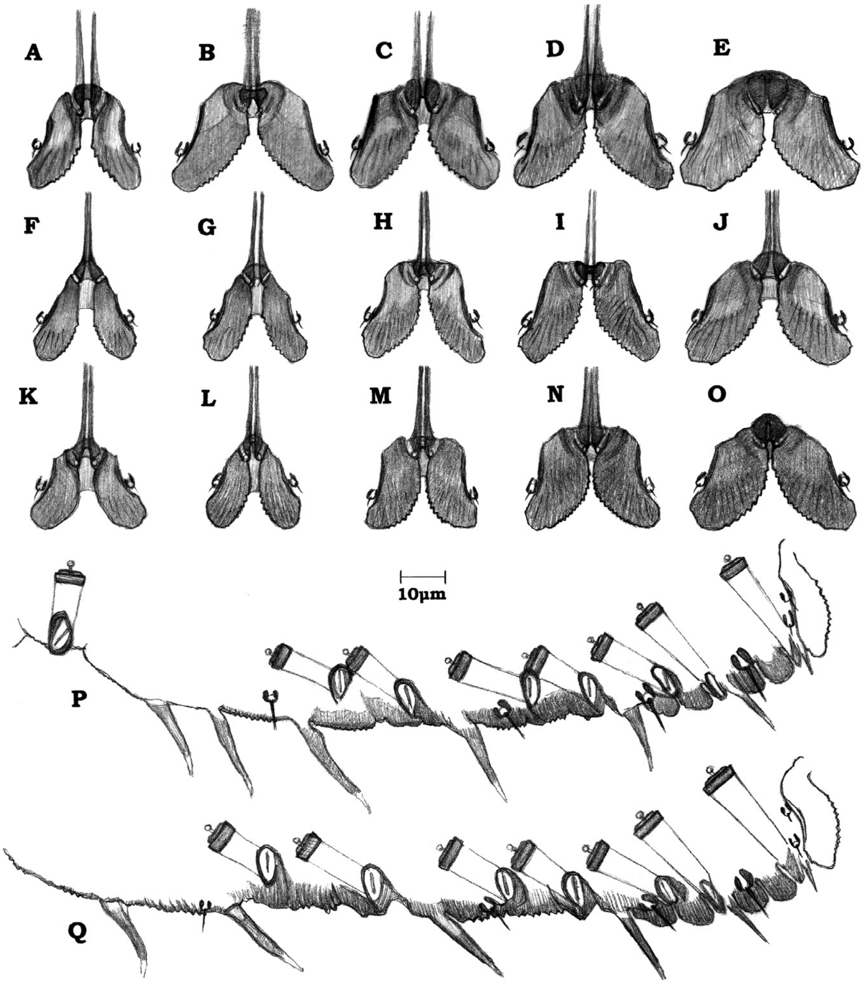

Fig. 10. *Aulacaspis tubercularis*, foliicolous (A–D, F–N, P, Q) and ramicolous (E, O) specimens. A–O, median trullae; P and Q, pygidial margin, dorsal surface. A–E and P, Group 1–3 (on Lauraceae); F–J and Q, Group 4; K–O, Group 6 (on *Mangifera*). A, [75NPL-217]; B, [88ML-326]; C, [78IND-160]; D and E, [83NPL-318]; F, [86ML-168]; G, [86ML-215]; H and I, [88ML-62]; J, [83NPL-107]; K, [78IND-64]; L, [92PL-124]; M–O, [83NPL-375]; P, [75NPL-217]; Q, [88ML-62].

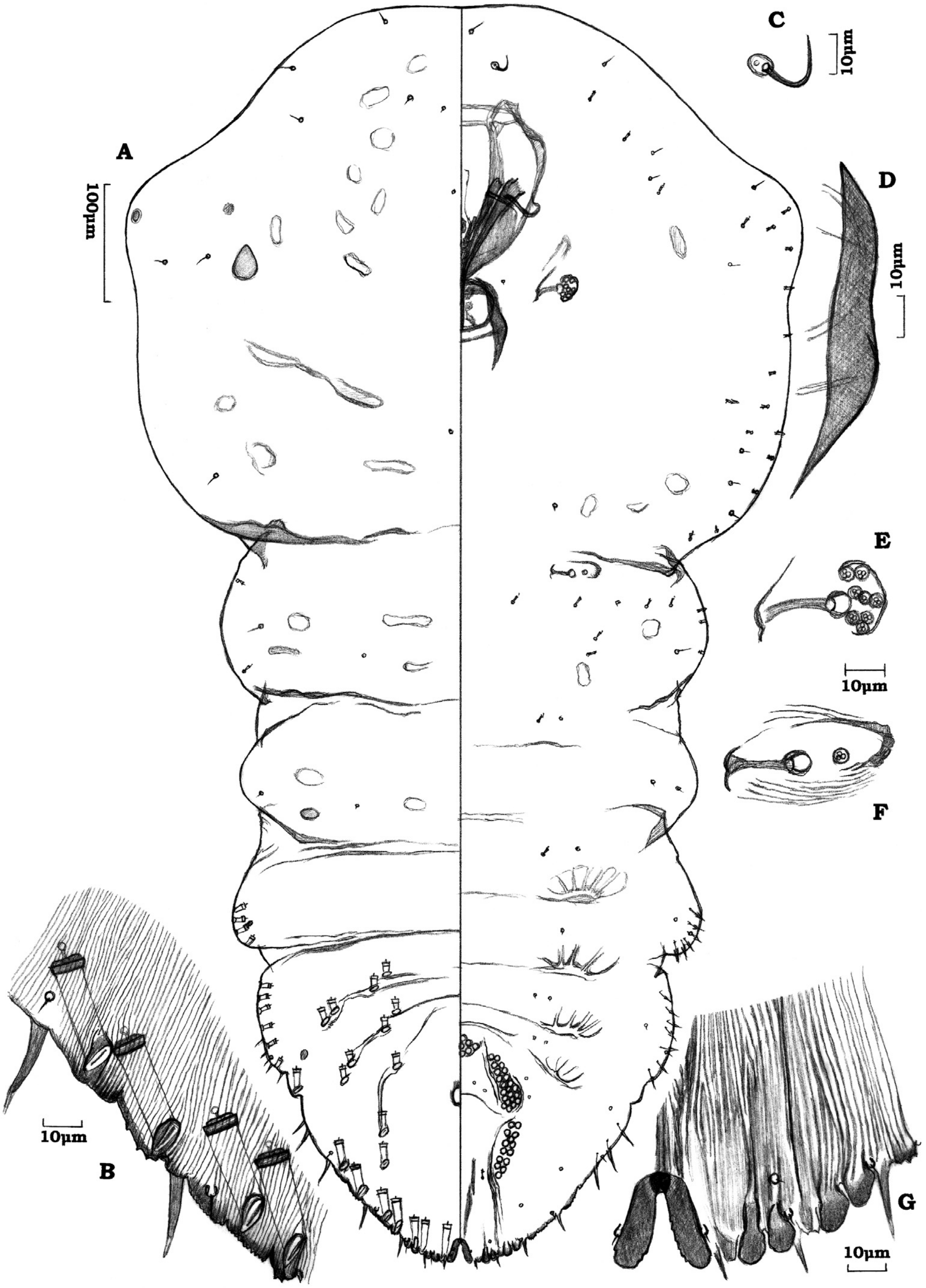

Fig. 11. *Aulacaspis alisiana*. A-li Shan, Taiwan, on *Neolitsea*. B, margin of abd IV and V, dorsal surface; C, antenna; D, peribuccal sclerosis; E, anterior spiracle; F, posterior spiracle; G, trullae.

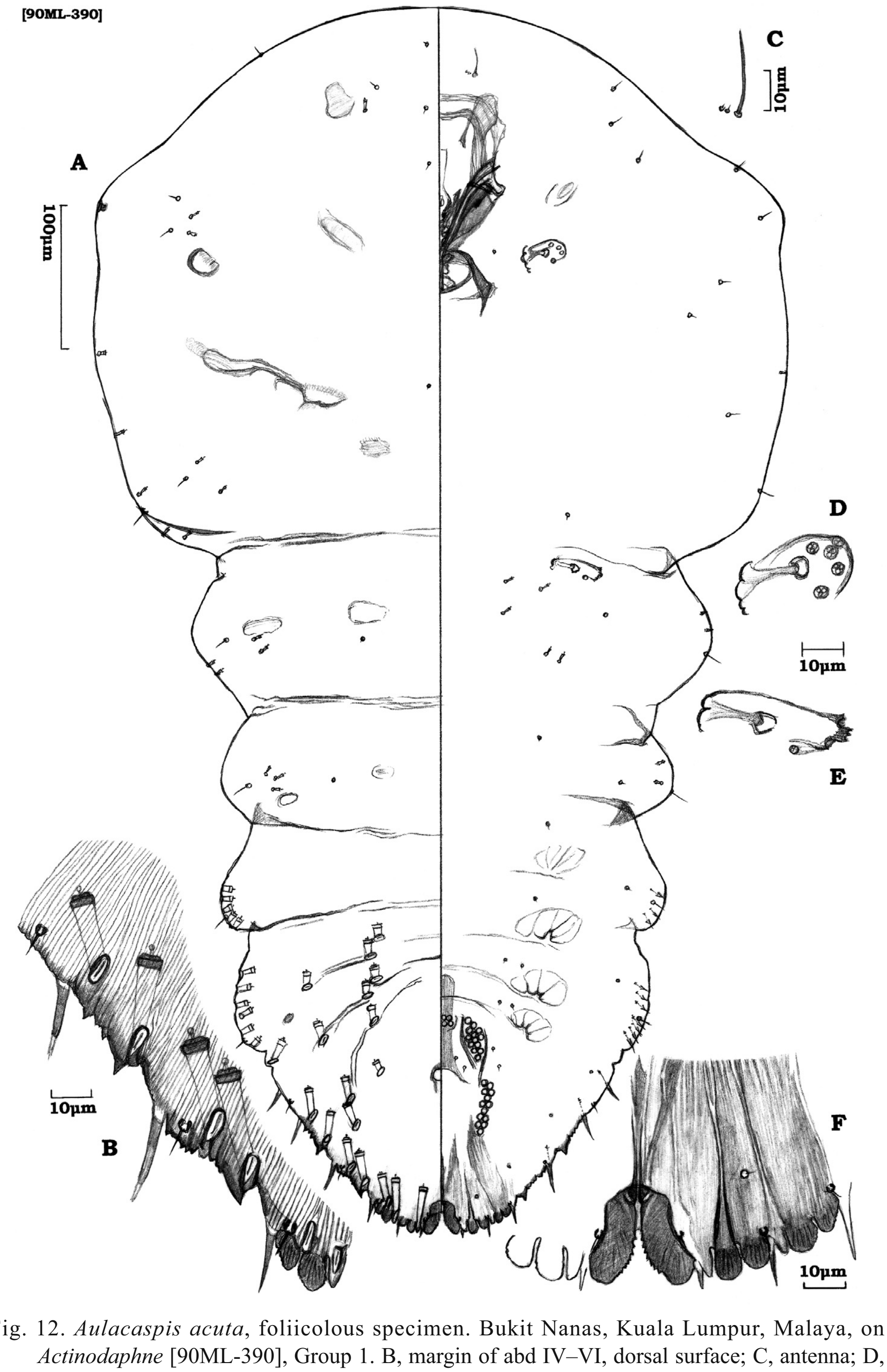

Fig. 12. *Aulacaspis acuta*, foliicolous specimen. Bukit Nanas, Kuala Lumpur, Malaya, on *Actinodaphne* [90ML-390], Group 1. B, margin of abd IV–VI, dorsal surface; C, antenna; D, anterior spiracle; E, posterior spiracle; F, trullae.

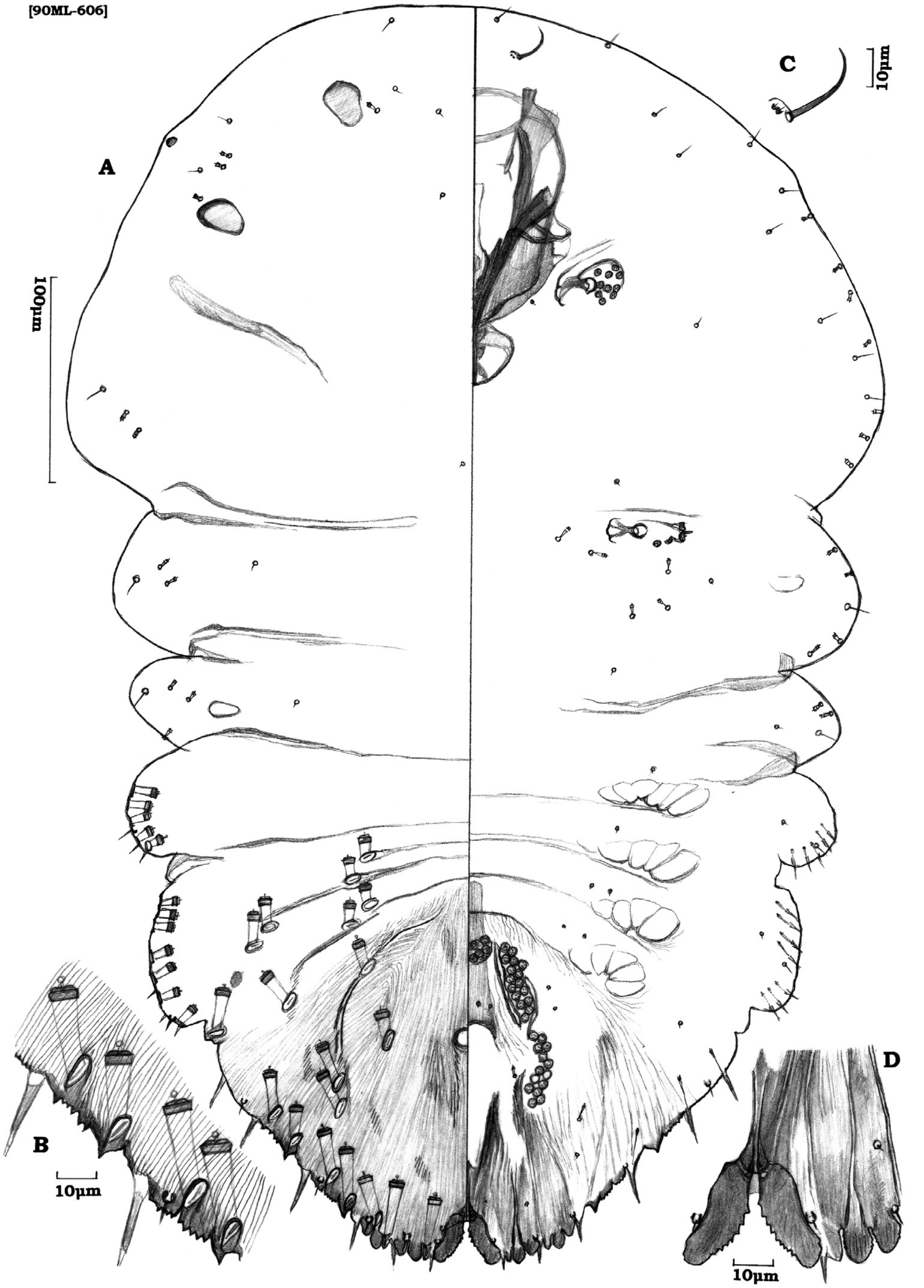

Fig. 13. *Aulacaspis acuta*, foliicolous specimen, teneral. Bukit Nanas, Kuala Lumpur, Malaya, on *Actinodaphne* [90ML-606], Group 1. B, margin of abd IV and V; C, antenna; D, median and second trullae.

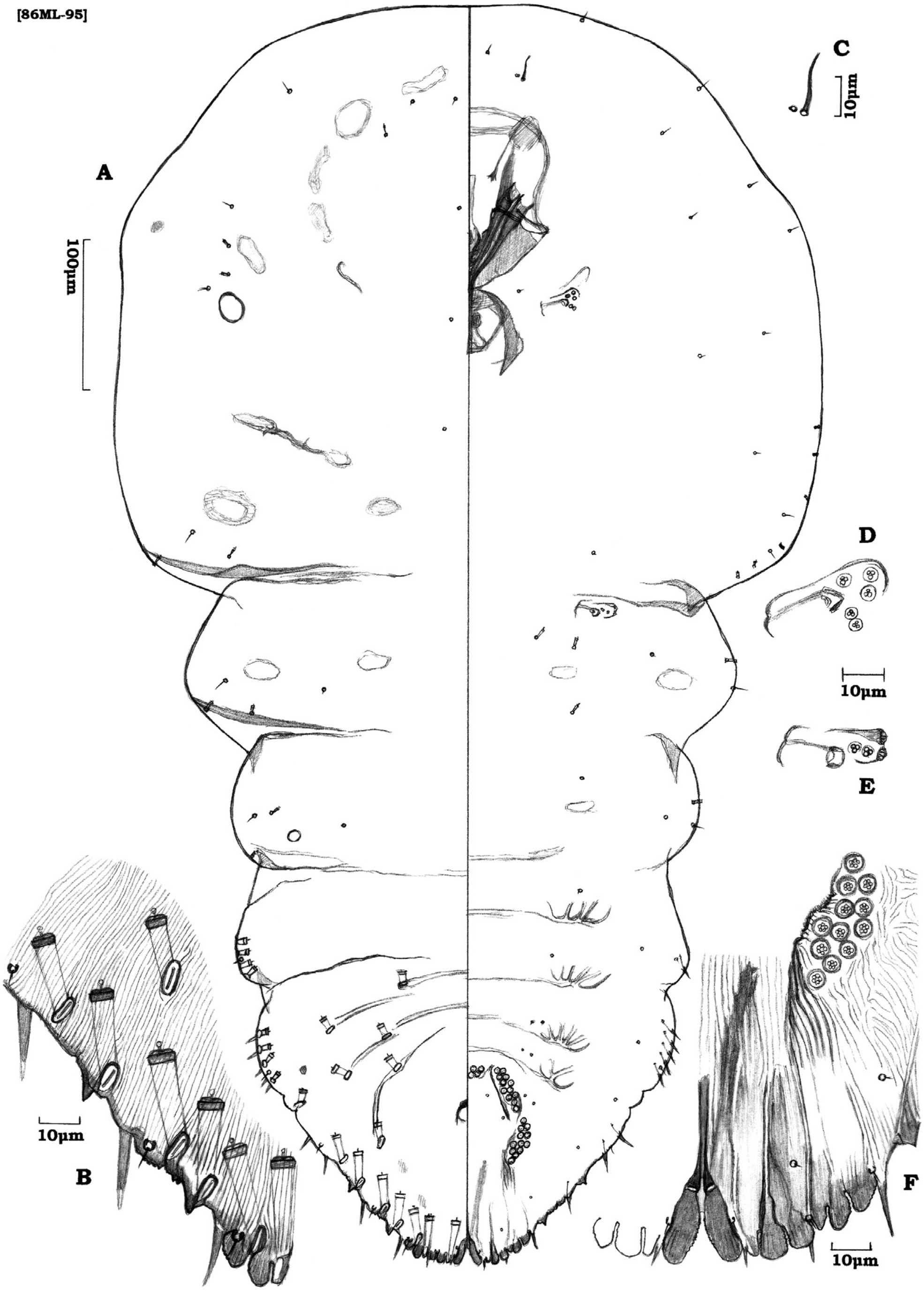

Fig. 14. *Aulacaspis acuta*, foliicolous specimen. Ulu Kali, Malaya, on *Neolitsea* [86ML-95], Group 2. B, margin of abd IV–VI, dorsal surface; C, antenna; D, anterior spiracle; E, posterior spiracle; F, trullae.

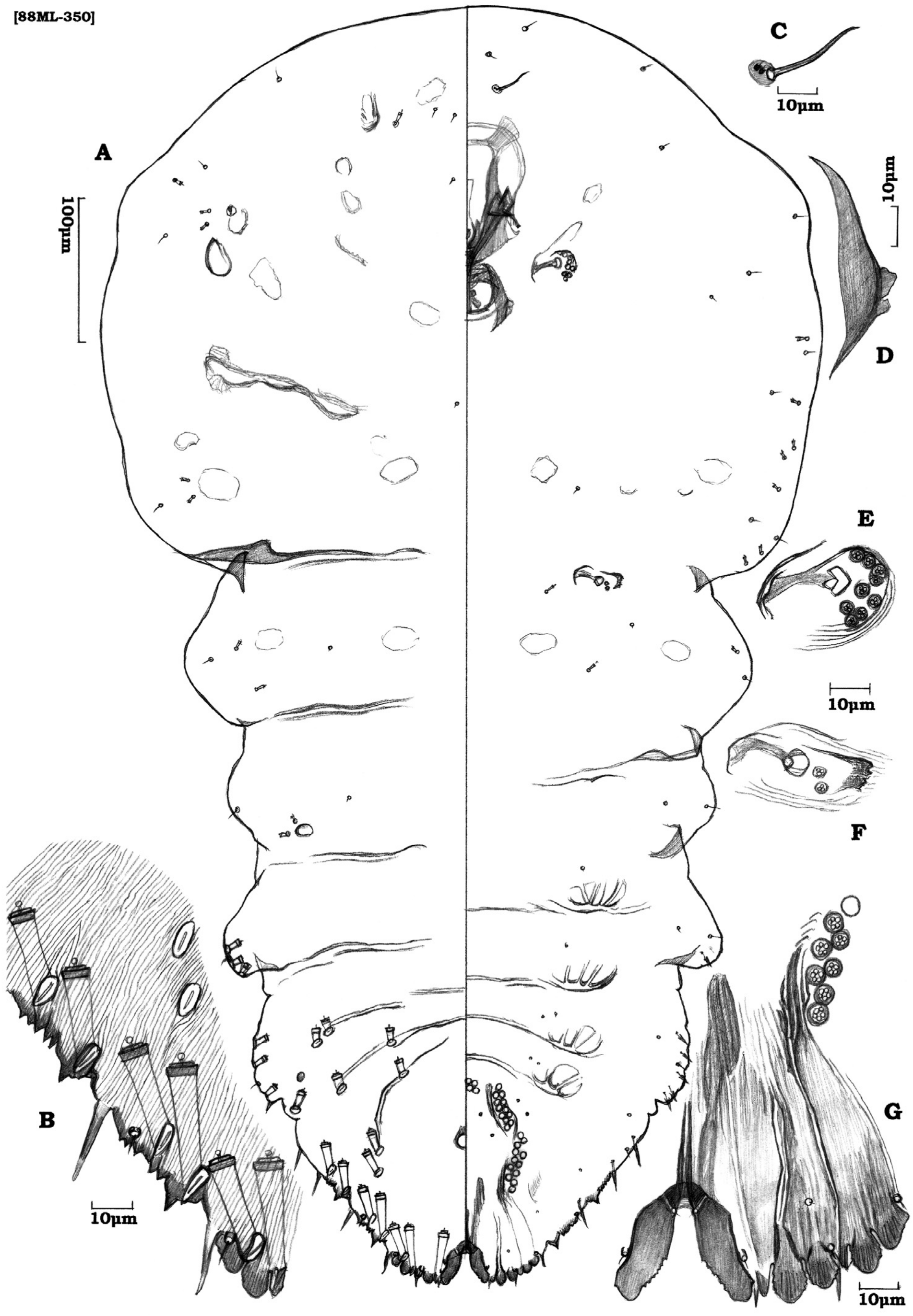

Fig. 15. *Aulacaspis acuta*, foliicolous specimen. Sepilok, Sabah, on *Alangium* [88ML-350], Group 5. B, margin of abd IV–VI, dorsal surface; C, antenna; D, peribuccal sclerosis; E, anterior spiracle; F, posterior spiracle; G, trullae.

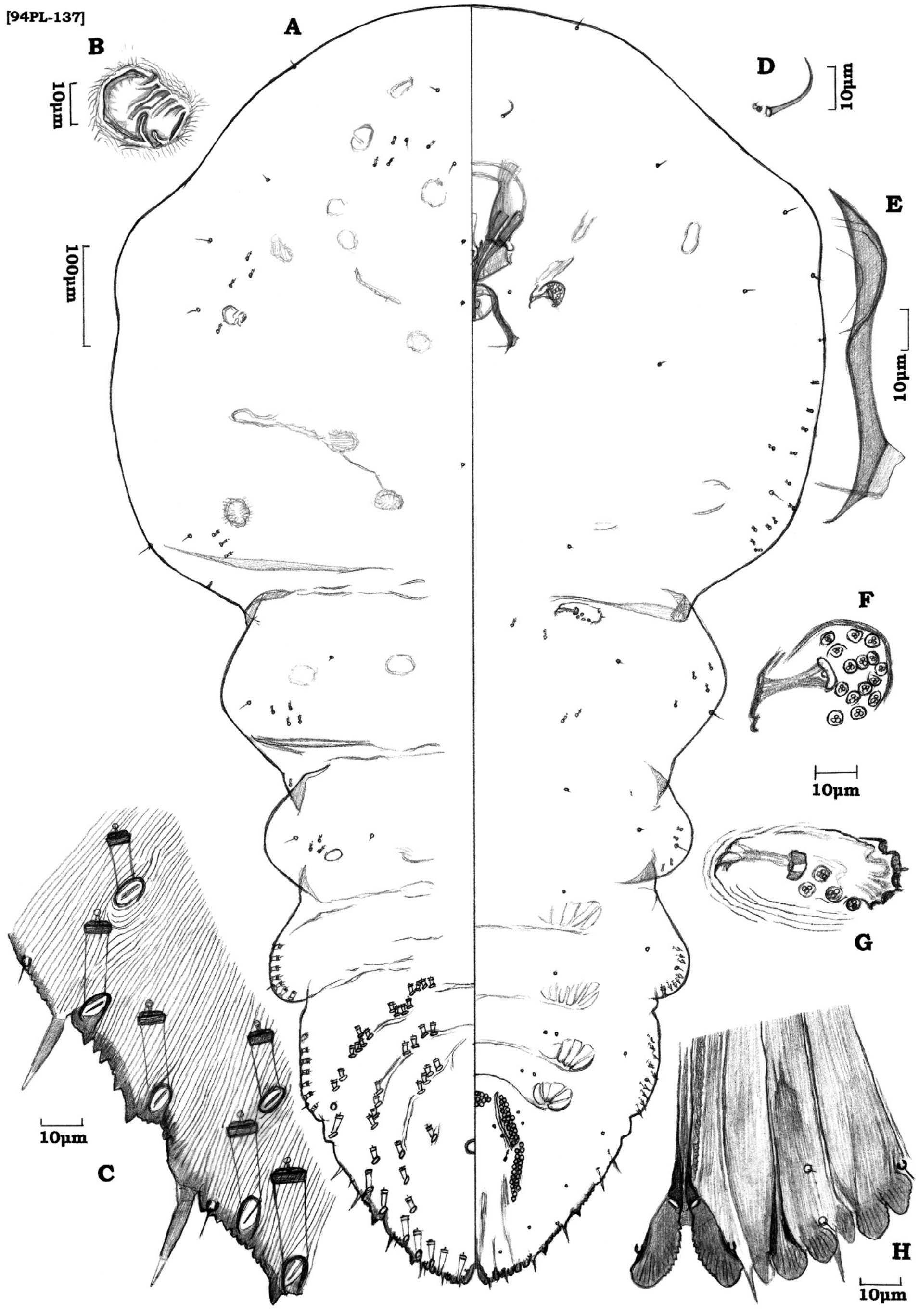

Fig. 16. *Aulacaspis acuta*, foliicolous specimen. Bataan, Luzón, on *Lepisanthes* [94PL-137], Group 7. B, dorsal scar on prothorax; C, margin of abd IV and V, dorsal surface; D, antenna; E, peribuccal sclerosis; F, anterior spiracle; G, posterior spiracle; H, trullae.

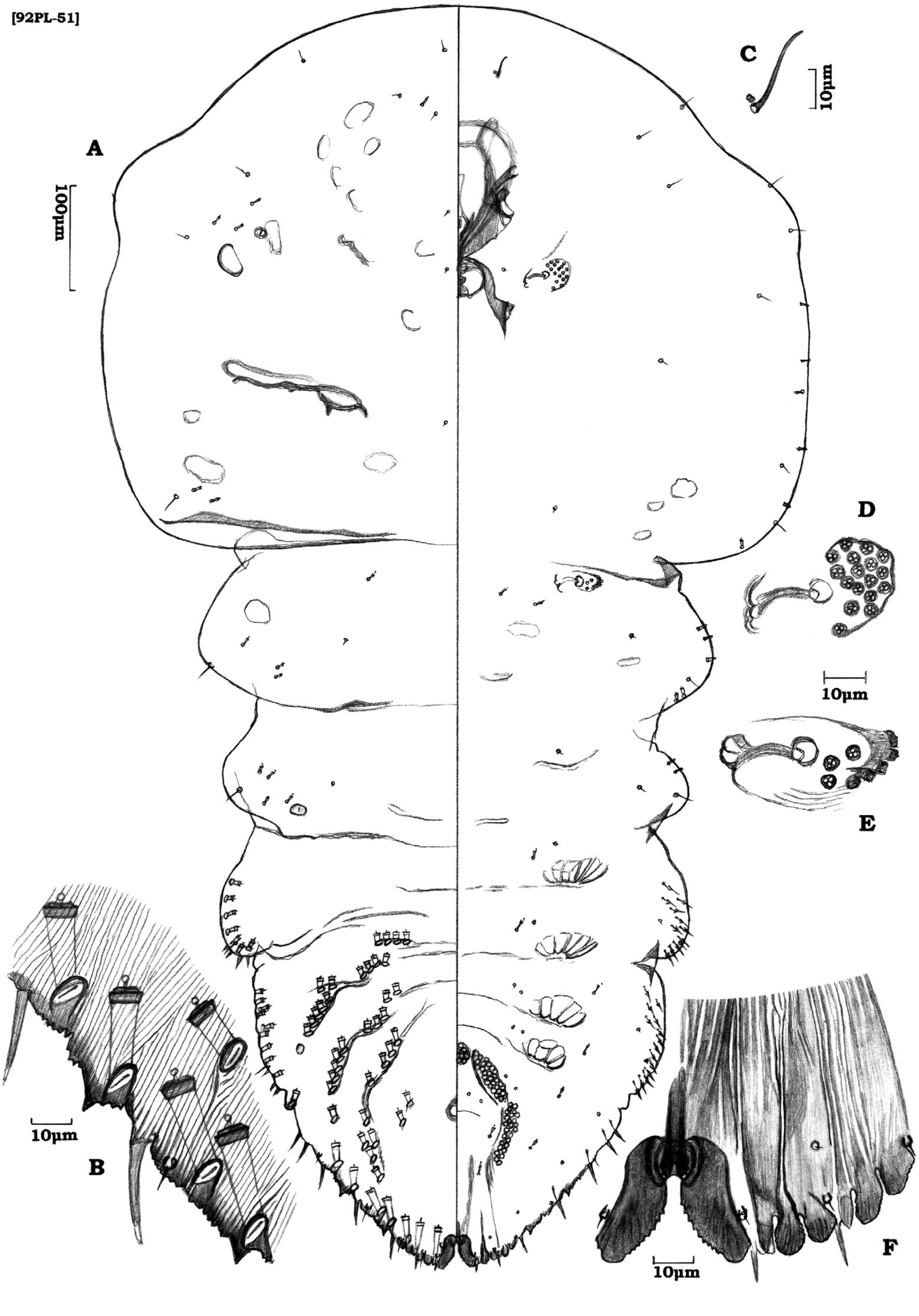

Fig. 17. *Aulacaspis acuta*, foliicolous specimen. Albay, Luzón, on *Guioa* [92PL-51], Group 7. B, margin of abd IV and V, dorsal surface; C, antenna; D, anterior spiracle; E, posterior spiracle; F, trullae.

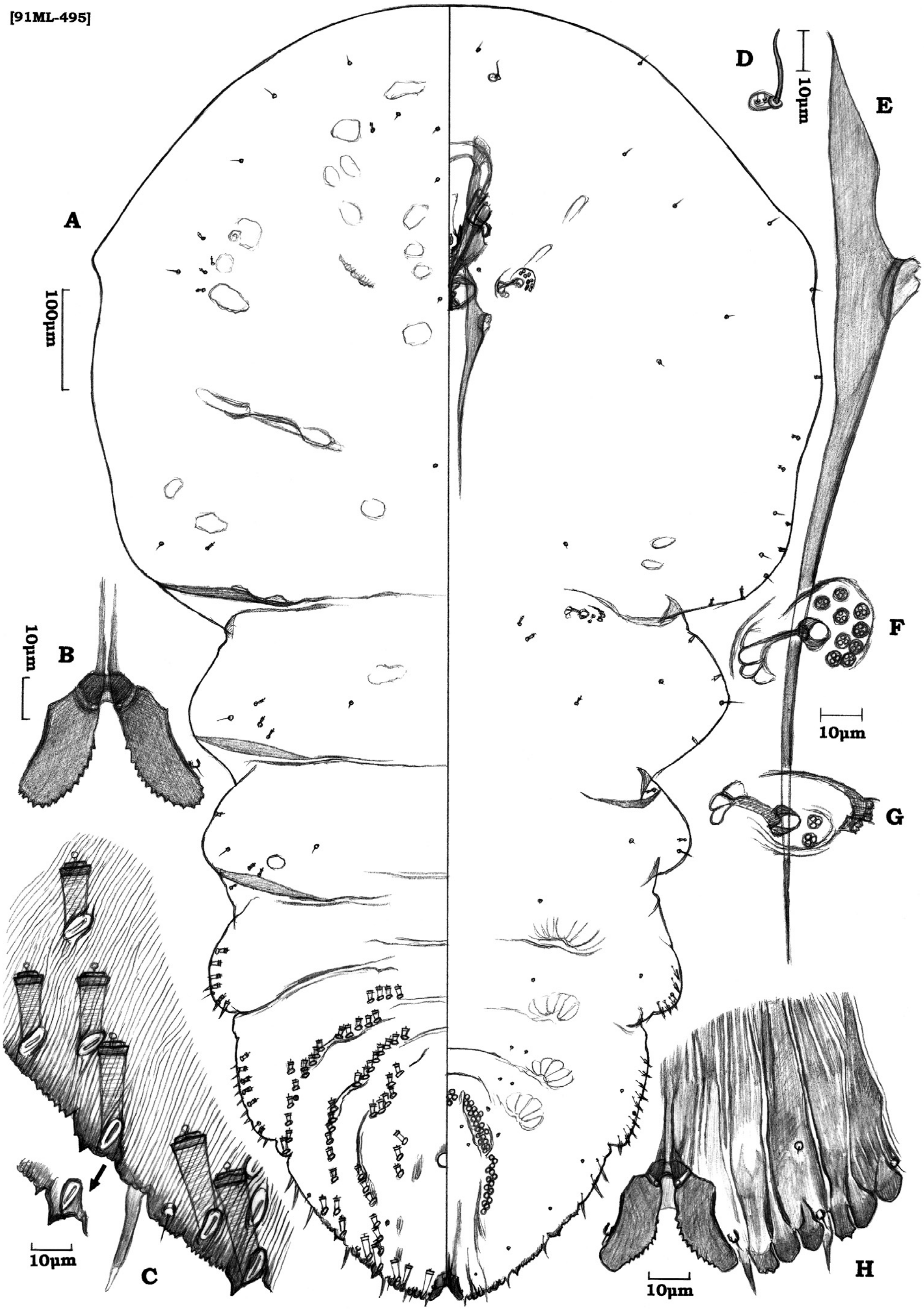

Fig. 18. *Aulacaspis acuta*, foliicolous (A, C–H) and ramicolous (B) specimens. Penang, Malaya, on *Scleropyrum* [91ML-495], Group 8. B, median trullae (ramicolous specimen); C, margin of abd IV and V, dorsal surface; D, antenna; E, peribuccal sclerosis; F, anterior spiracle; G, posterior spiracle; H, trullae.

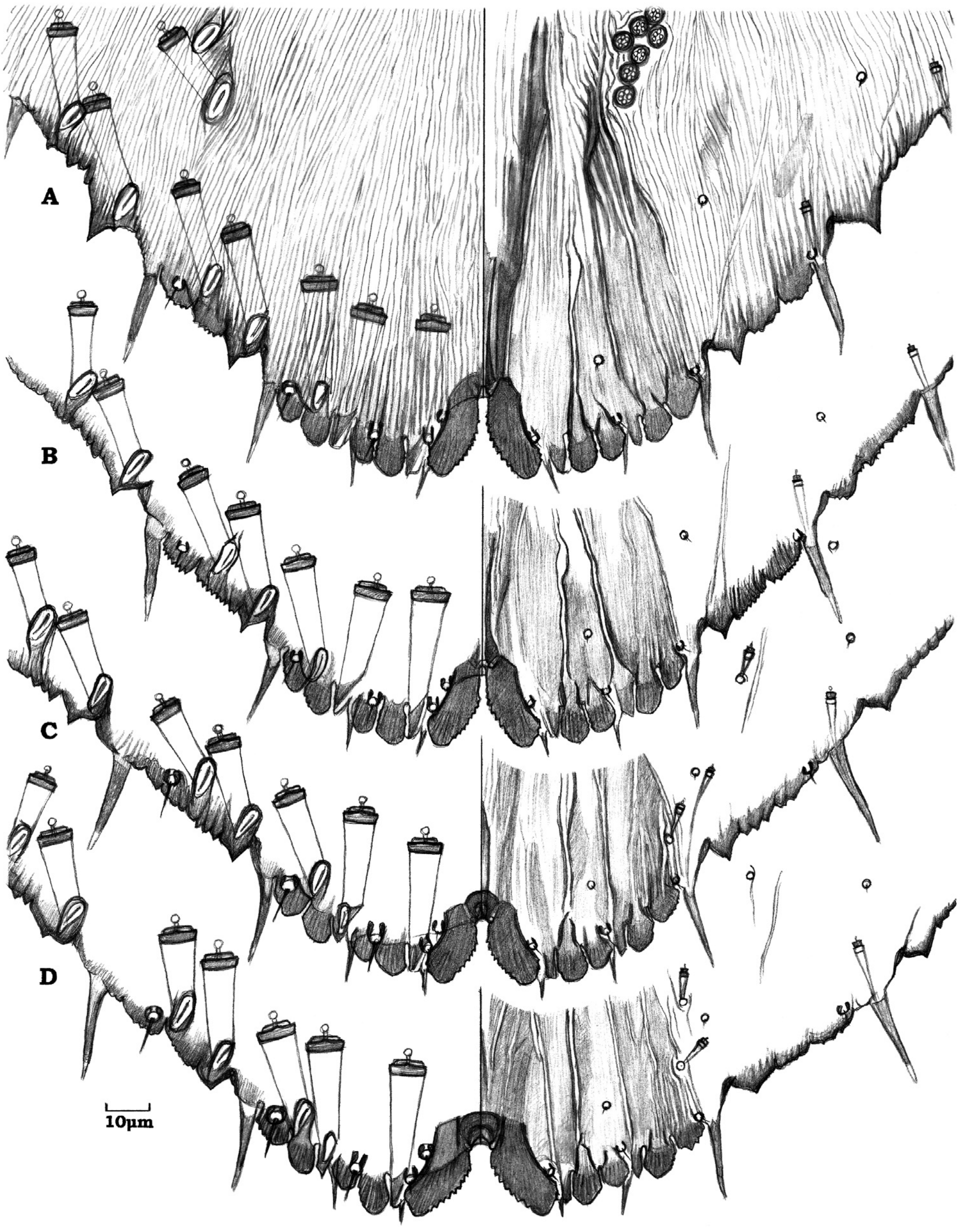

Fig. 19. *Aulacaspis acuta*, foliicolous (A, B) and ramicolous (C, D) specimens collected at the same locality: Ulu Kali, Malaya. A, on *Actinodaphne* [86ML-484], Goup 2; B–D, on *Cinnamonum* [86ML-4], Group 2. Pygidial margin, 4 examples.

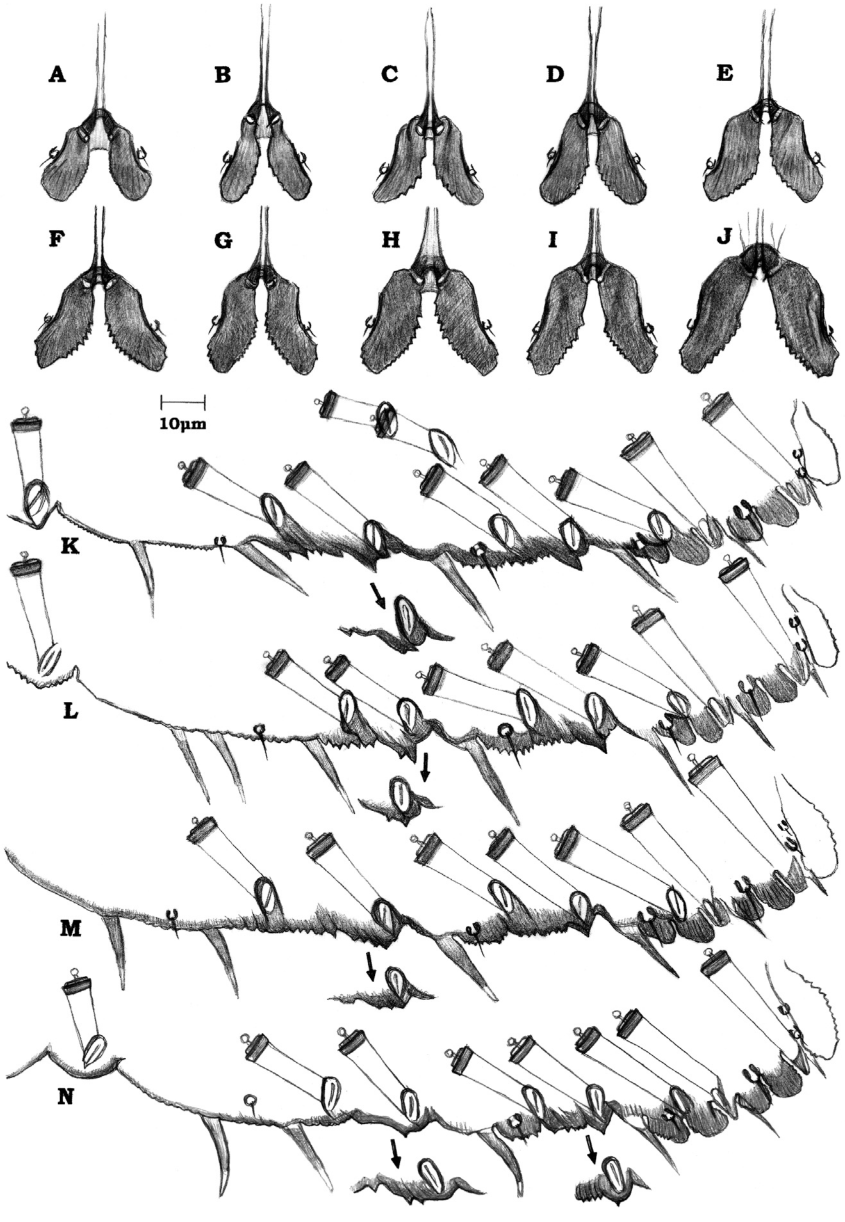

Fig. 20. *Aulacaspis acuta*, foliicolous specimens. A–J, median trullae; K–N, pygidial margin, dorsal surface. A, [94PL-19], Group 6; B, [90ML-153], Group 6; C, [92SP-28], Group 5; D, [86ML-100], Group 5; E, [91ML-495], Group 8; F, [93PL-140], Group 5; G and H, [90ML-346], Group 5; I and J, [88ML-350], Group 5; K, [94PL-19], Group 6; L, [90ML-153], Group 6; M, [86ML-100], Group 5; N, [88ML-142], Group 3.

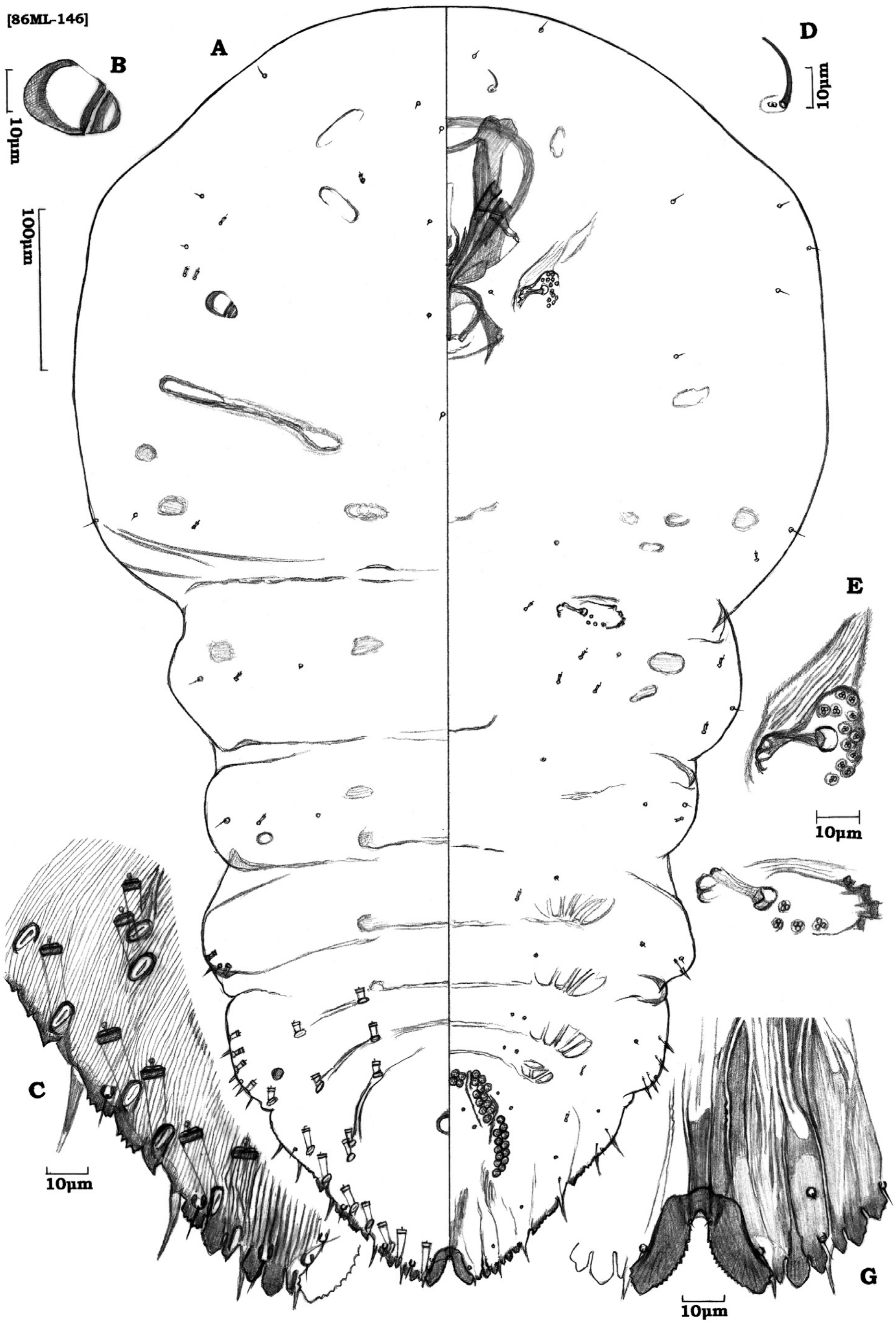

Fig. 21. *Aulacaspis taipingensis*, foliicolous specimen. Taiping, Malaya, on *Cinnamomum* [86ML-146]. B, dorsal scar on prothorax; C, pygidial margin, dorsal surface; D, antenna; E, anterior spiracle; F, posterior spiracle; G, trulla.

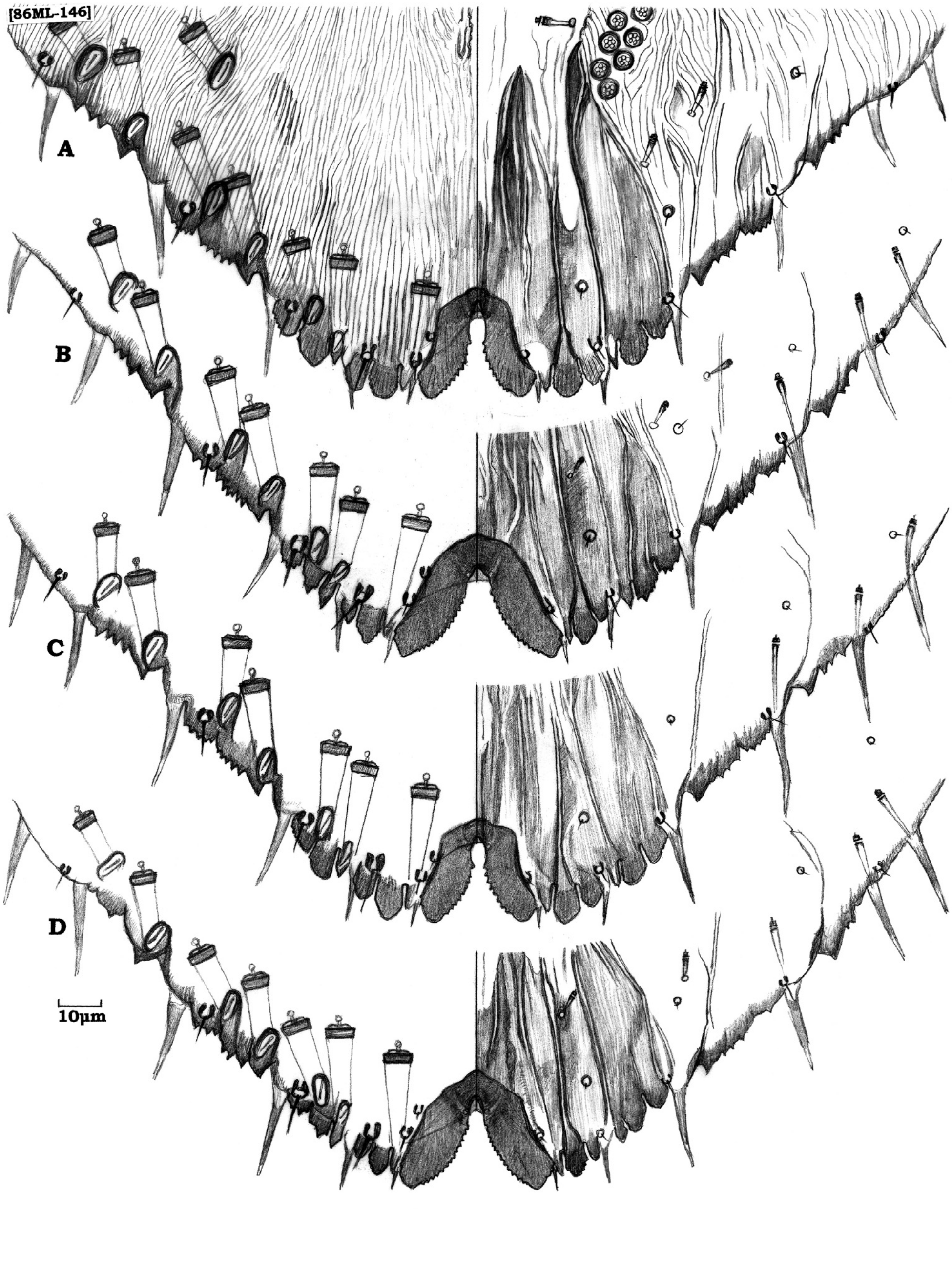

Fig. 22. *Aulacaspis taipingensis*, foliicolous (A, B) and ramicolous (C, D) specimens. Taiping, Malaya, on *Cinnamomum* [86ML-146]. Pygidial margin, 2 examples from foliicolous subsample and 2 from ramicolous subsample. A and C, Type P; B and D, Type D.

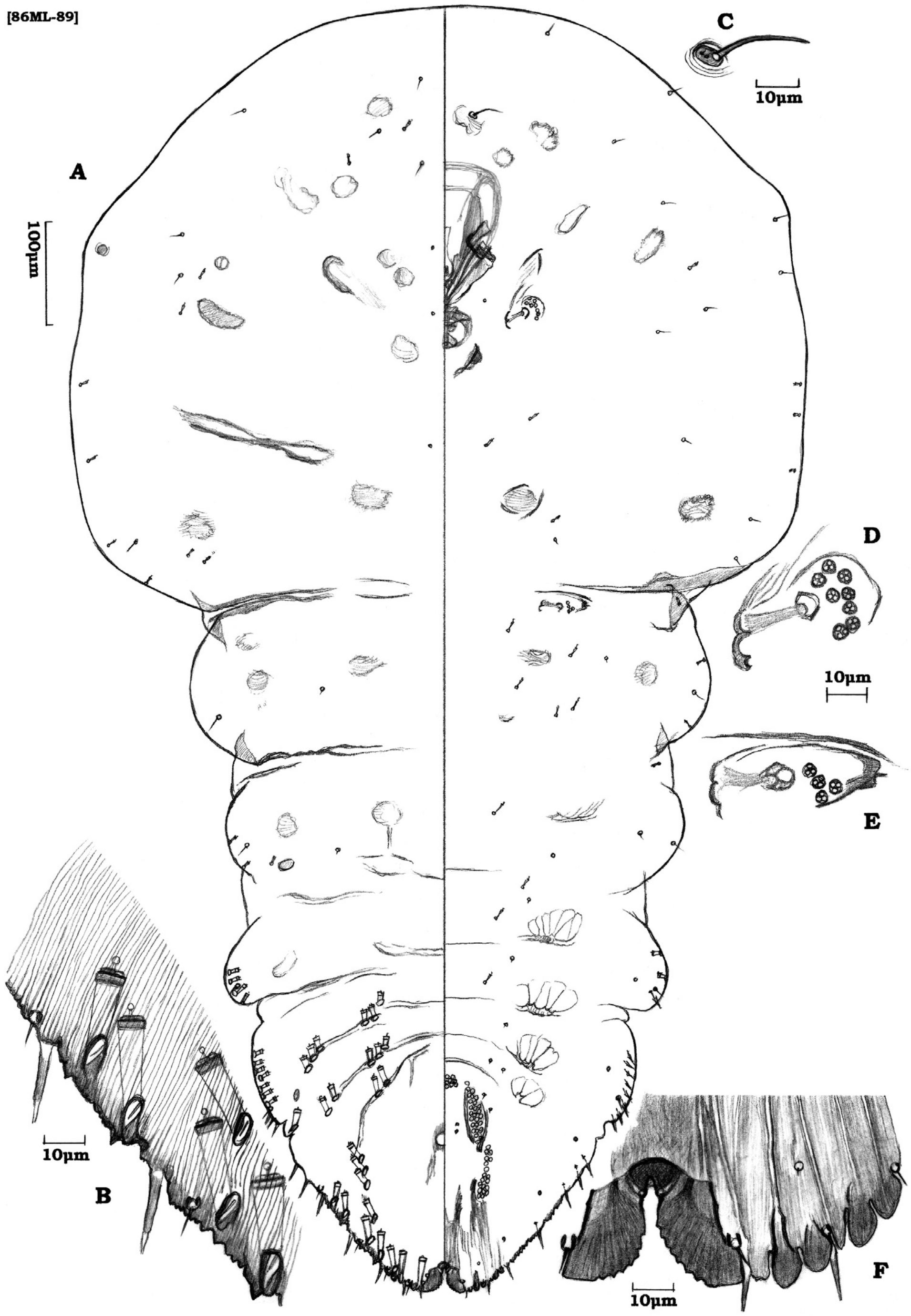

Fig. 23. *Aulacaspis alyxiae*. Ulu Kali, Malaya, on *Alyxia* [86ML-89]. B, margin of abd IV and V, dorsal surface; C, antenna; D, anterior spiracle; E, posterior spiracle; F, trullae.

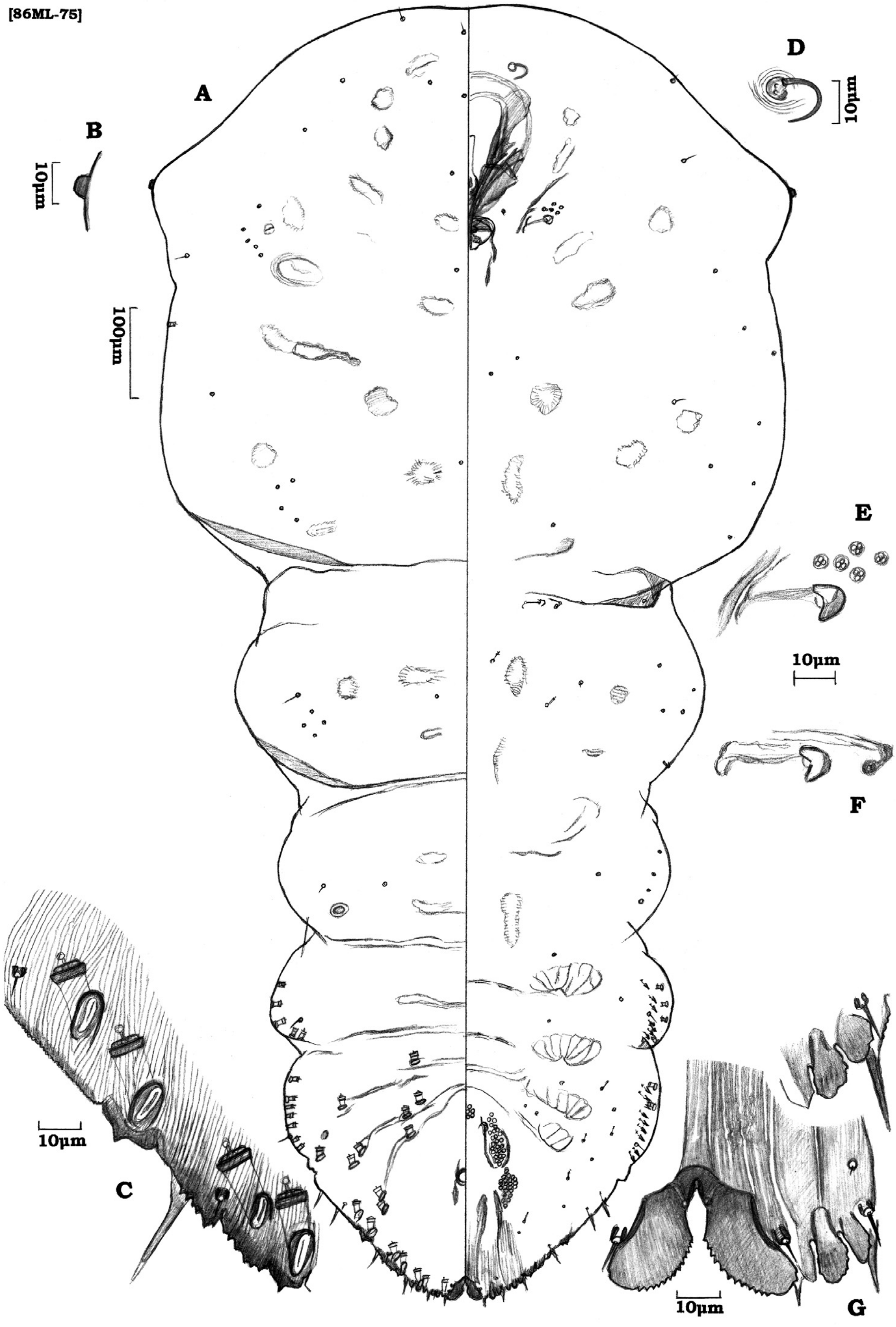

Fig. 24. *Aulacaspis scurrulae*. Ulu Gombak, Malaya, on *Scurrula* [86ML-75]. B, eye-spot; C, margin of abd IV and V; D, antenna; E, anterior spiracle; F, posterior spiracle; G, trullae.

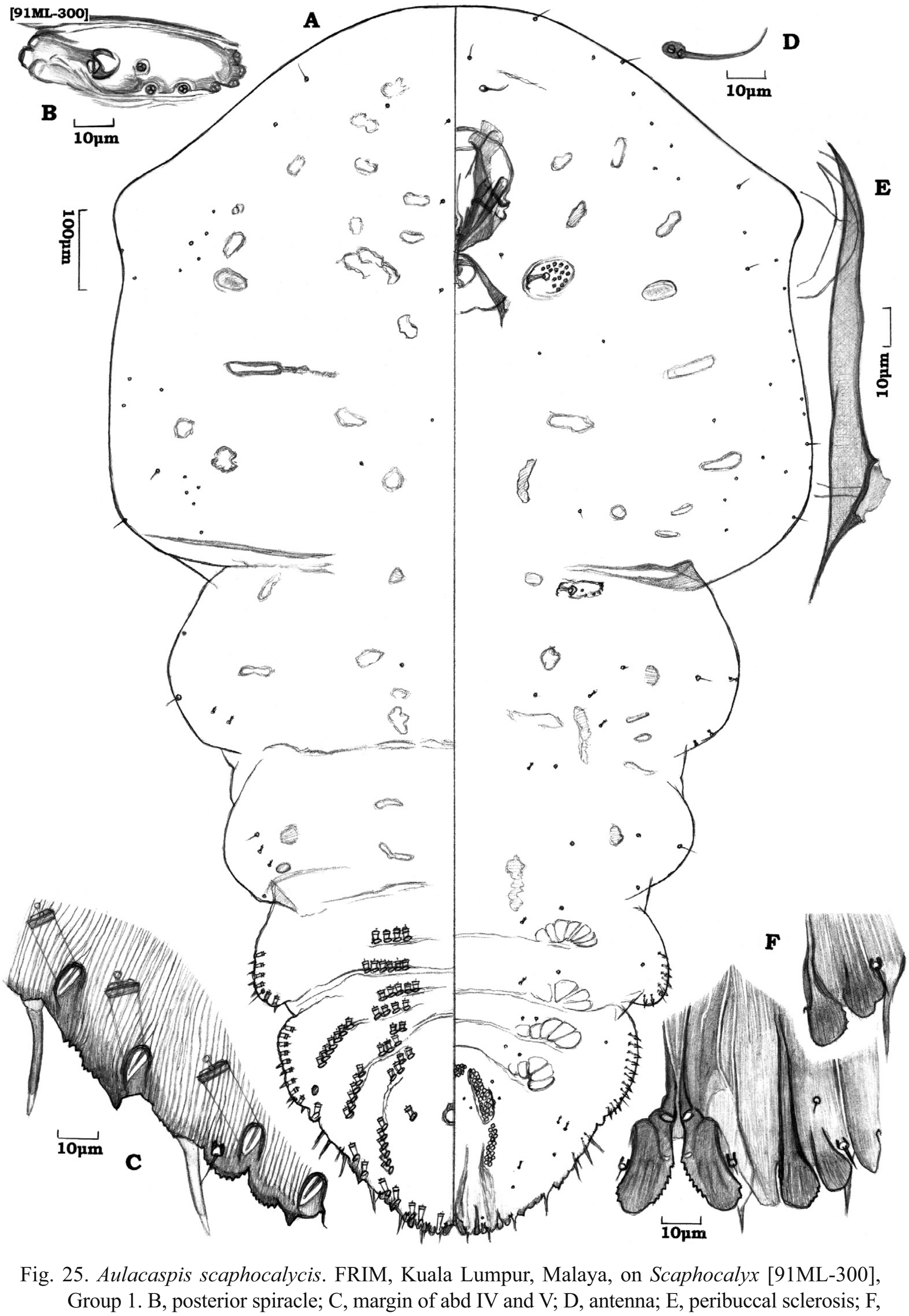

Fig. 25. *Aulacaspis scaphocalycis*. FRIM, Kuala Lumpur, Malaya, on *Scaphocalyx* [91ML-300], Group 1. B, posterior spiracle; C, margin of abd IV and V; D, antenna; E, peribuccal sclerosis; F, trullae.

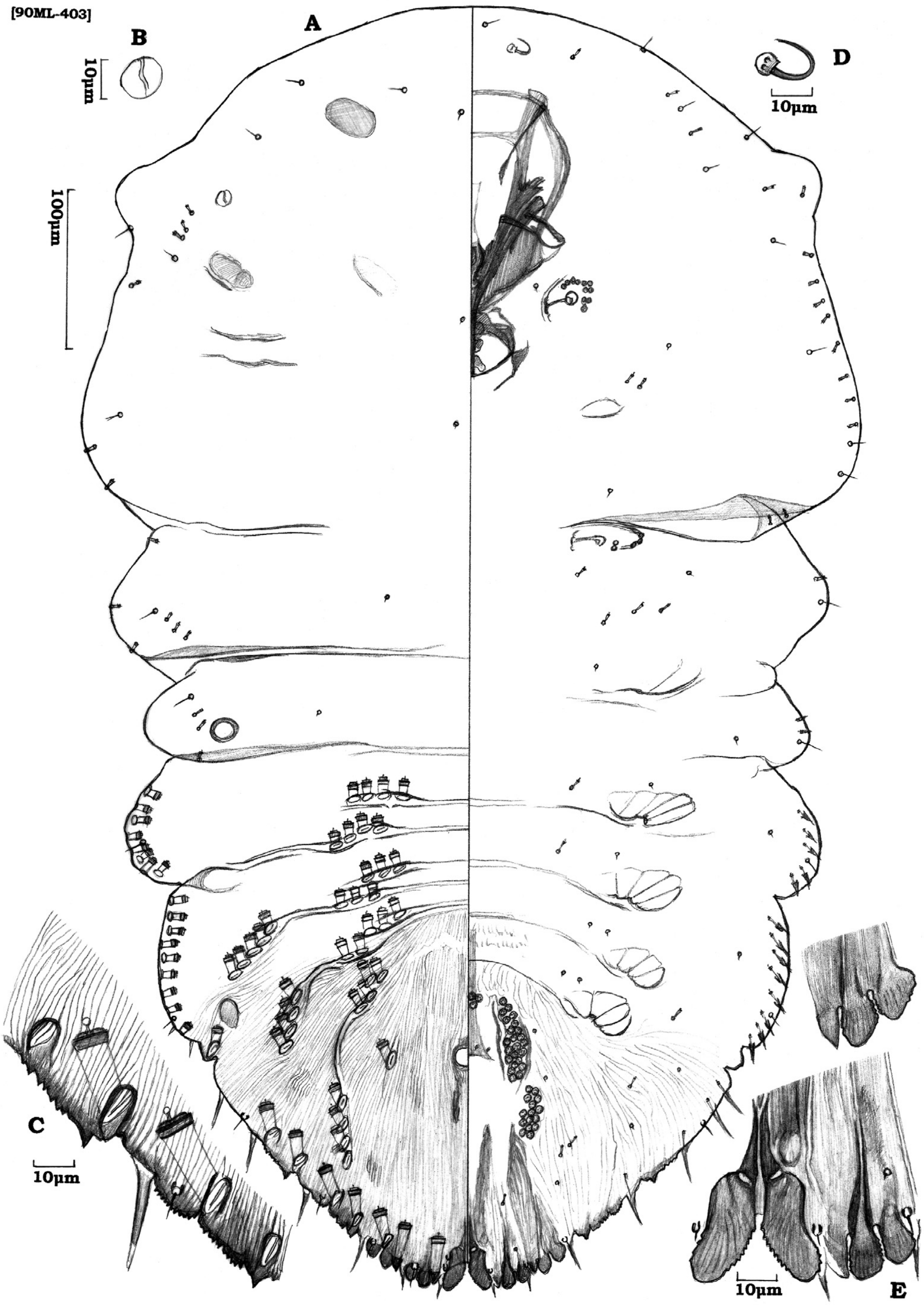

Fig. 26. *Aulacaspis scaphocalycis*, teneral. Bukit Nanas, Kuala Lumpur, Malaya, on *Scaphocalyx* [90ML-403], Group 2. B, dorsal scar on prothorax; C, margin of abd IV and V, dorsal surface; D, antenna; E, trullae.

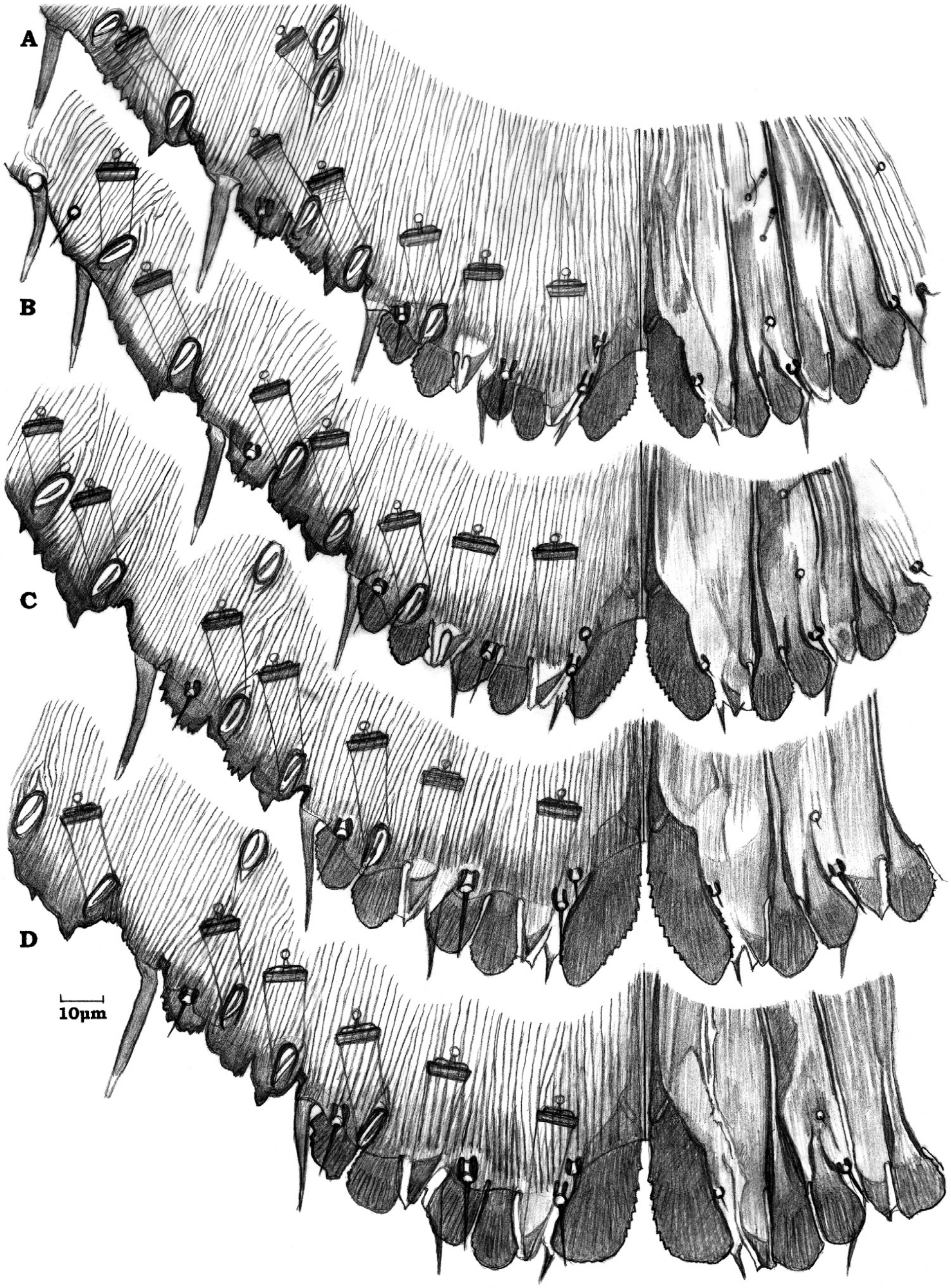

Fig. 27. *Aulacaspis scaphocalycis*. A, Bukit Nanas, Kuala Lumpur, Malaya, on *Ryparosa* [90ML-583], Group 2; B, Bukit Fraser, Malaya, on *Sandoricum* [86ML-329], Group 4; C and D, Bukit Fraser, on *Xanthophyllum* [86ML-345], Group 4. Pygidial margin, 4 examples.

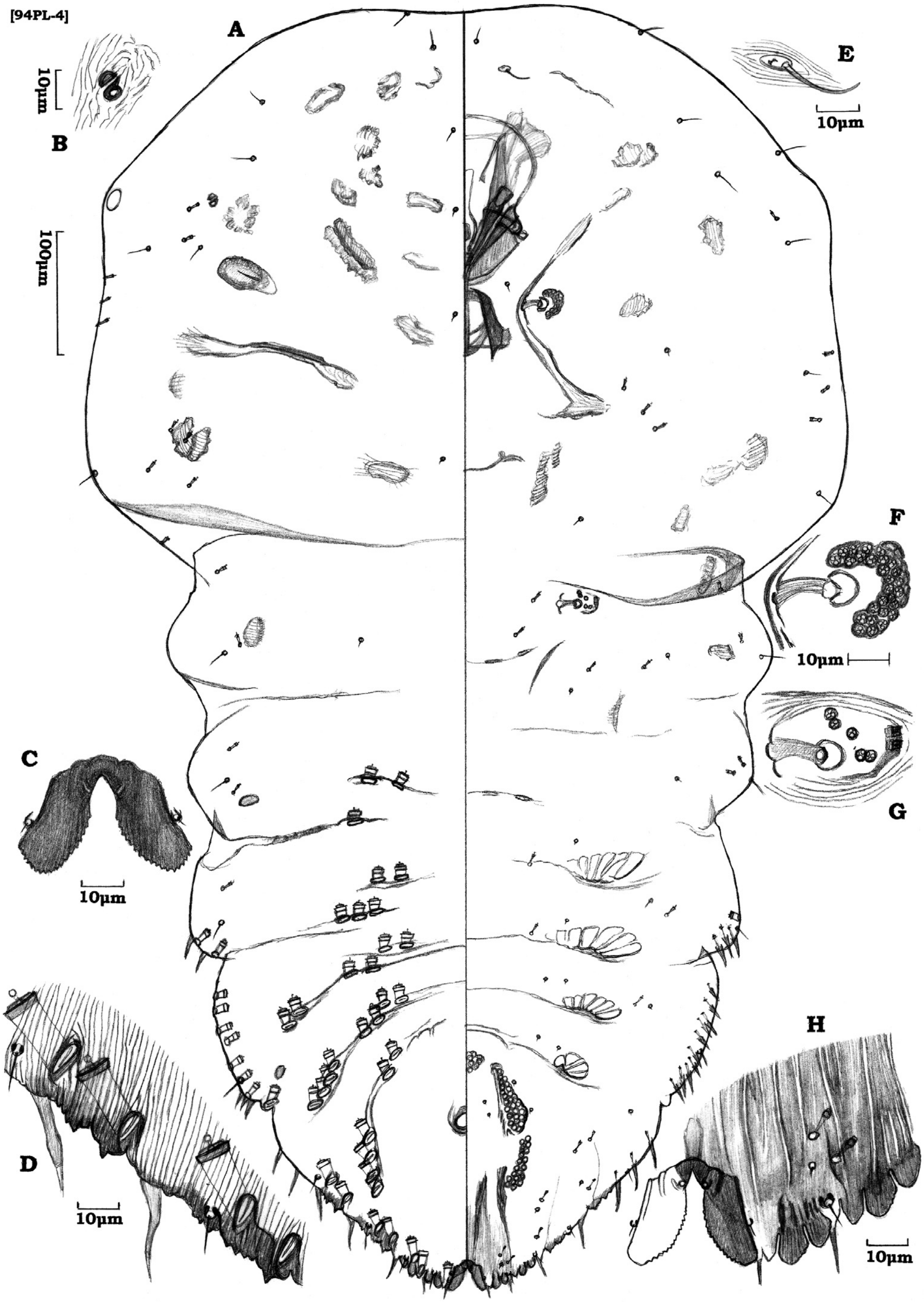

Fig. 28. *Aulacaspis lagunae*, foliicolous (A, B, D–H) and ramicolous (C) specimens. Mt. Makiling, Luzón, on *Cinnamomum* [94PL-4]. B, dorsal scar on prothorax; C, median trullae (ramicolous specimen); D, margin of abd IV and V, dorsal surface; E, antenna; F, anterior spiracle; G, posterior spiracle; H, trullae.

[94PL-4]

Fig. 29. *Aulacaspis lagunae*, foliicolous specimen, teneral. Mt. Makiling, Luzón, on *Cinnamomum* [94PL-4]. B, margin of abd IV and V, dorsal surface; C, trullae.